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Review

A Global Analysis of Climate Change and the Impacts on Oyster Diseases

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Abstract: Recently, global demand for seafood such oysters is increasing as consumers seek healthy and nutritive alternatives to a diet dominated by animal protein. This trend is attributed to the growing interest in sustainable seafood strategies and a surge in customer demand. Despite oysters being one of the most promising seafoods, the oyster industry faces various challenges, such as increased infectious diseases promoted by climate change, pollution, and environmental burdens. Hence, the industry's current challenges must be addressed to ensure long-term viability. One of the current challenges in the production industry (in response to climate change) is mortality or poor product quality from microbial infection. This review reveals that climate change fosters pathogen development, significantly impacting disease spread, host susceptibility, and the survival rates of oysters. Rising temperatures, driven by climate, create favourable conditions for bacteria and viruses to multiply and spread quickly, making oysters more susceptible to diseases and ultimately adversely affecting the oyster industry. Climate-induced changes in oyster-associated microbes and pathogens, coupled with disruptions in biochemical pathways and physiological functions, can lead to increased disease outbreaks and reduced survival in the industry, impacting production and profitability. These adverse effects could result in decreased oyster supply, potentially affecting seafood markets and prices, and necessitate additional investments in disease management strategies. This review identifies and highlights how aquatic pathogens promoted by climate change will affect the oyster industry on a global scale. This review also presents an in-depth global assessment of climate change's impacts on oysters relative to their disease exposure and pathogen spread and identifies possible future directions.

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1. Introduction

Aquaculture is one of the most promising food sectors to provide the world's population with animal protein sources and tackle the problem of food scarcity caused by overpopulation [1]. Oysters have gained global popularity due to their demand as an essential seafood, leading to increased production in recent years [2]. This trend is attributed to the growing interest in seafood options and a surge in customer demand [3]. Oyster production has emerged as a significant sector in several nations worldwide. Several oyster species are commercially produced, including the Pacific oyster (*Crassostrea gigas*), New Zealand rock oyster *(Saccostrea glomerata*), European flat oyster *(Ostrea edulis*), and as previously, Eastern oyster *(Crassostrea virginica*) (Figure 1). *Crassostrea gigas* is the most commonly cultivated species in commercial enterprises across many countries [4,5]. This widespread cultivation is due to the species' desirable characteristics, such as its large size, rapid growth rate, and high meat yield. *Crassostrea virginica* is exclusively cultivated in the United States, Canada, and Mexico [6], whereas *Saccostrea glomerata* is only grown in Australia [7]. Only a few European countries, the United States, and South Africa, can produce *Ostrea edulis* in limited quantities [8,9].

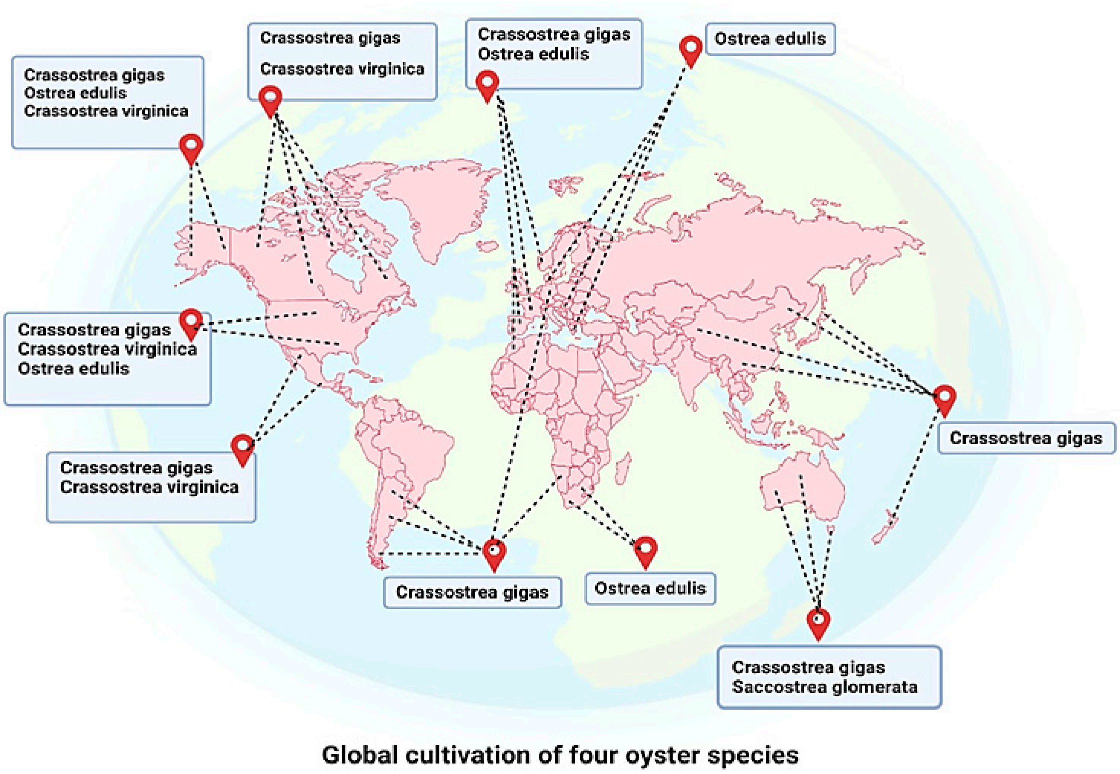

Figure 1. Global cultivation of four oyster species; *C. gigas* is grown in the greatest number of countries, spanning North and South America, Western Europe, and Australia, while *S. glomerata* is only grown in Australia. *C. virginica* is exclusively grown in North America, whereas *O. edulis* is grown in the USA, some European countries, and South Africa.

Oyster farming is mainly concentrated in Asia, with China leading the way, accounting for more than 80% of global production. Besides Asia, significant oyster production also occurs in North America, Europe, and Oceania [10,11]. In 2020, the United Nations Food and Agriculture Organization (FAO) reported that global oyster production increased from 5.2 million metric tonnes in 2015 to 5.6 million [12].

The global oyster output will continue to rise in the following years, driven by increased consumer demand and the spread of sustainable aquaculture practices [12]. However, oyster production faces various challenges, including increased infectious diseases, environmental burdens, and especially climate change [13,14]. In this regard, the industry's current challenges must be addressed to ensure its long-term viability and sustainability. One of these challenges is the changes in the manifestation of oyster pathogens promoted by climate change.

In the last decades, climate change and its intricate interactions have taken on a worldwide significance [15]. Every day, greenhouse gases in the atmosphere rise, impacting all ecosystems, including aquatic animals [16]. Furthermore, with rising ambient temperatures, water temperature simultaneously changes, which makes aquatic organisms more vulnerable to pathogenic diseases changes to environment conditions [17]. Marine experts once thought that overfishing posed the biggest threat to oysters. However, it is now revealed that climate change-induced disease also threatens global oyster populations [18]. Climate change has brought substantial alteration to the aquatic environment. The environmental alterations include increased temperature, acidification, and sea-level rise, leading to the submergence of low-lying regions, intensified flooding, and salinity intrusion into freshwater areas [19]. The intricate connections among these environmental alterations result in various expressions of stress and diseases in marine organisms, including oysters [20].

One of the challenges encountered through alteration to the aquatic environment is the impact on aquatic animal diseases, which also expands in range in freshwater and marine waters [21–23]. Over the years, studies have indicated that climate change can increase pathogen development and consequently influence disease spread, host susceptibility, and survival. In addition, some infectious oyster diseases spread faster with increasing water temperature, which could directly impact human health [24].

Oyster production is commonly carried out in coastal and estuarine sites, making it challenging to forecast, regulate, and confine infectious disease outbreaks [12,25]. Furthermore, managing the spread of pathogens is complicated because of the ability of marine pathogens to rapidly spread over large distances in aquatic habitats compared to terrestrial environments [26].

Oyster diseases are increasingly being linked to environmental factors such as temperature. Outbreaks tend to be more severe in tropical areas, possibly because many disease-causing pathogens thrive in warmer waters [27,28]. Specifically, the temperature alteration can cause a shift in the growth rates and spatial dispersion of various aquatic pathogens, thereby increasing the severity and frequency of oyster disease outbreaks [29]. In addition, climate change can influence other ecological variables that mediate between aquatic pathogens and oyster diseases [30]. Also, variations in precipitation patterns and the elevation of sea levels can potentially modify the salinity levels within estuaries, thereby influencing the proliferation and dispersion of aquatic pathogens and their consequent effects on the oyster population. In the last century, the global temperature has experienced an increase of 0.6 degrees Celsius [31]. Future projection shows a further increase of 2 to 4 degrees Celsius at the end of this century [32]. The increase in temperature presents a significant threat to aquatic organisms, including oysters and the marine ecosystem [33]. The physical ocean environments are experiencing significant impacts, resulting in various adverse effects on the physiology of oyster populations [34–36]. Climate change causes a cascade of ecological impacts, including the proliferation of microbial/pathogenic populations. This phenomenon may create ideal conditions for pathogens to thrive and multiply quickly. Thus, the oyster sector may face considerable challenges due to increased microbial populations, such as harmful algal blooms (HABs). These HABs produce toxins that can accumulate in oysters, making them unsafe for human consumption [37]. As a result, oyster farmers require strict monitoring and mitigation measures to safeguard their livelihoods and the consumers' health. In addition, the escalating microbial threats highlight the urgency of addressing climate change and its cascading effects on various industries, including the vital oyster sector.

To adequately tackle the issue of climate change, understanding the dynamics of pathogen distribution and interactions with essential climate variables is crucial. Moreover, a collaborative global endeavour is necessary, prioritizing scientifically rigorous management strategies considering marine ecosystems' complex and interconnected nature [38,39]. Establishing effective management techniques can be challenging due to the complex interplay between different aspects [40,41].

Therefore, identifying and highlighting how aquatic pathogens will affect oysters in the face of climate change is essential. Furthermore, it is crucial to establish the current knowledge of these impacts on a global scale. Hence, this study aims to present an in-depth global assessment of climate change impacts on oysters relative to their disease exposure and pathogen spread via changing water temperature, salinity, and pH and also identifies possible future directions.

2. Climate Change and Oyster Development

The increasing levels of CO_2 in the atmosphere due to climate change are causing ocean acidification. When CO_2 dissolves in seawater, carbonic acid is formed, lowering the ocean's pH. In their early stages of development, oysters are vulnerable to acidic conditions [42]. Ocean acidification affects the ability of oyster larvae to form calcium carbonate shells, making them weaker and more susceptible to diseases [43]. Oysters rely on calcium carbonate for formation; thus, developing and maintaining their shells in acidic environments becomes harder, potentially leading to weaker shells and decreased survival rates [42,43].

Climate change has also resulted in rising sea temperatures, which can affect oyster growth and reproduction. Elevated temperatures can disrupt the timing of spawning and larval development, possibly reducing oyster recruitment rates and population dynamics [44,45]. Oysters are influenced by their surroundings regarding body temperature (ectothermic). As global temperatures increase due to climate change, oysters may experience stress, impacting their growth, development, and reproductive abilities [46].

Salinity levels play a role in oyster growth rates and shell development. Higher salinity promotes growth and better shell formation, while lower salinity levels lead to weaker shells. Hence, climate change can affect oysters' well-being and size by altering their salinity levels [43,44]. This, in turn, makes them more vulnerable to pathogens and diseases. Additionally, changes in salinity during the larval stages can significantly impact the survival of oyster larvae. Such events could affect oyster habitats, directly disrupting their feeding patterns and creating adverse conditions for their development [18].

3. Impacts of Ocean Acidification on Oysters' Physiology

Ocean acidification and heat can affect the microbiome of *S. glomerata* and increase oysters' susceptibility to various diseases [47–49]. This change can negatively affect oysters' shell-building ability and disrupt the intestinal microbiome [26,50], thus resulting in reducing diversity and abundance of helpful bacteria and increasing harmful ones [51]. Oysters may become less able to digest and absorb nutrients due to this alteration in the microbiome, which might make them more susceptible to bacterial and viral diseases. Figure 2 shows how the microbial community in oysters may be impacted by the warming water, perhaps leading to an increase in pathogenic bacteria and viruses that might affect their health [52,53].

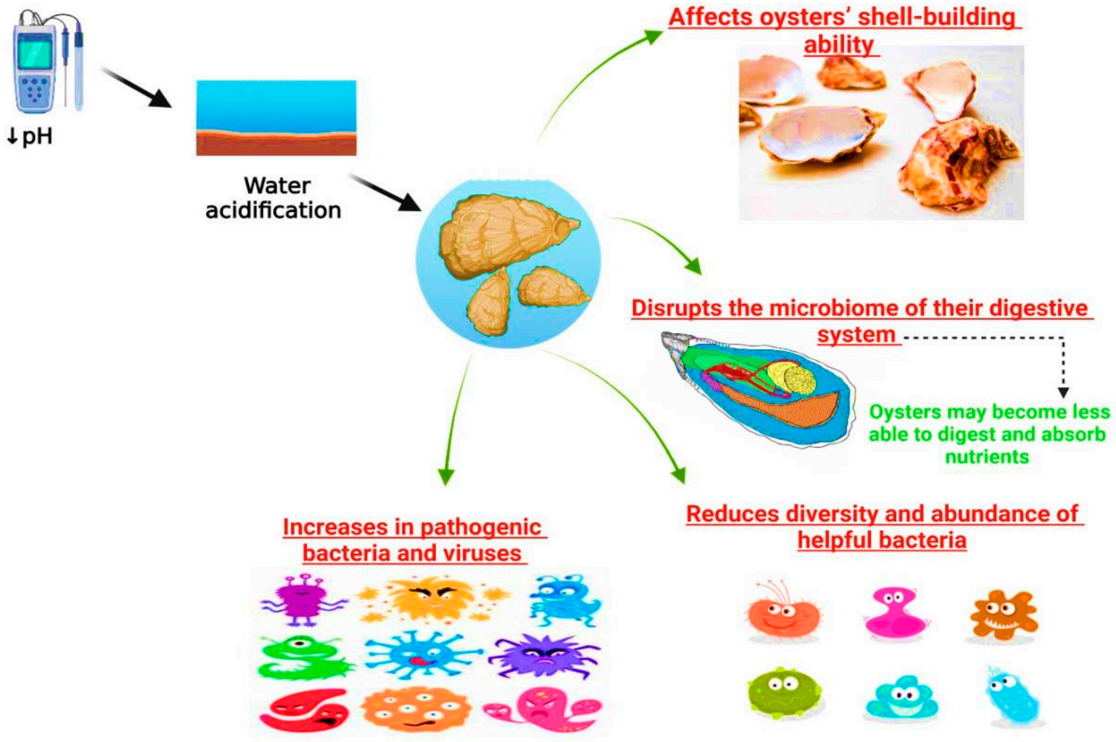

Figure 2. Impacts of ocean acidification on oyster physiology. This modification might be relative to increases in pathogenic bacteria and virus, reduces diversity and an abundance of beneficial effects, and finally alters the microbiota.

The expression of viral genes, including catalase, peroxiredoxin 6, and ecSOD, has been reported to increase in oysters exposed to high CO_2 levels over some generations [54]. The transgenerational (B2) oysters, renowned for their disease resistance and rapid growth, exhibit the most significant changes. According to [54], prolonged exposure to high CO_2 levels can significantly change oyster gene expression. Additionally, research demonstrates that elevated CO_2 levels might affect gene expression, compromising vital physiological functions such as metabolism and immunological response [55,56]. The sensitivity of oysters to diseases has also increased due to excessive salinity, which has led to a diminished immune system and, thus, increased mortality throughout the hot summer [57]. Recently, Li et al., suggested that this change might attribute to increasing oxidative stress/apoptosis genes and microbiota dysbiosis when oysters are exposed to continuous high-temperature-induced ocean acidification [58].

In areas of drought, the water's salinity and dissolved solids concentration increase, leading to stress in oysters. The stress can reduce the oysters' immunity, making them more susceptible to diseases. Hot summer months can further increase the oysters' stress levels, leaving them vulnerable to infections. Furthermore, high water temperatures can create favourable conditions for the growth of harmful bacteria and viruses, which can infect the oysters and cause disease-related mortality.

The selective breeding of oyster families for rapid development and disease resistance enables them to alter their calcite crystal bio-mineralization pathways, supporting resilience to acidification and contributing to their adaptability [59]. According to [59], wild-type families of Sydney rock oysters (*Saccostrea glomerata*) exhibit higher shell bio-mineralization levels than bred families. Thus, selective breeding in oysters could be an effective global mitigation approach for sustainable shellfish production to survive upcoming changes in habitat acidity brought on by climatic factors.

Ocean acidification can impact the physiological reactions of native and non-native species of oysters [60]. Both species (*Magallana gigas* and *Ostrea edulis*) experienced increased metabolic rates and energy demand due to the temperature rise, but elevated pCO_2 did not have a similar impact. This result implies that anthropogenic CO_2 emissions can vary stress levels among oyster species. Also, persistent CO_2 emissions may adversely affect the structure and functioning of *M. gigas* [60]. This, in turn, will have significant ecological and economic implications, particularly for the aquaculture industry [60,61]. In the Pacific oyster (*Crassostrea gigas*), long-term (60 days) CO_2 exposure can significantly increase gene expression in DNA or RNA binding and suggests that transcription might begin after long-term CO_2 exposure.

On the other hand, short-term oyster treatment can lead to significant intracellular calcium variation and oxidative stress [35]. However, prolonged CO_2 exposure may allow oysters to revert to normal levels (physiological adjustment) of H_2O_2 in blood, intracellular calcium, and ROS level in hemocytes [35]. This, therefore, indicates that exposure to CO_2 can impact the expression of genes through changes in the regulation of transcription factors and modifications in the epigenetics of DNA or RNA-binding proteins [55]. One way in which CO_2 exposure can affect gene expression is by modifying the activity of transcription factors. These proteins bind to specific DNA sequences and control the expression of neighbouring genes [62]. Several studies have reported that CO_2 exposure can enhance the activity of some transcription factors, such as hypoxia-inducible factor-1 (*HIF-1*) and nuclear factor kappa B (*NF-κB*), which regulate many genes related to inflammation, oxidative stress, and cell growth [27,63]. On the other hand, gene expression can be affected by CO_2 exposure through changes to DNA accessibility and modifications in the epigenetics of DNA- and RNA-binding proteins [35,64].

Higher levels of apoptosis and the formation of reactive oxygen species (ROS) in hemocytes linked to ocean acidification may occur when oysters are exposed to high concentrations of PCO_2 [34,65]. Most notably, high PCO_2 levels can considerably negatively influence their immune systems, suggesting that higher PCO_2 levels may be linked to increased disease vulnerability in bivalves [34]. High amounts of PCO_2 can alter water pH and disturb the delicate balance of physiological processes the immune system depends on to protect against disease, impairing oysters' immune systems [60,66]. Oysters are especially vulnerable to changes in pH because their shells, which are essential for protection against predators and environmental stressors, rely on the process of calcification, which low pH levels can disrupt. The impact of high PCO_2 levels on oyster immune systems is a complex process involving various physiological and biochemical mechanisms. Nevertheless, maintaining stable pH levels in marine environments is crucial for the health and survival of oysters and other marine organisms.

Ocean acidification is characterized by the uptake of elevated CO_2 levels from the atmosphere into the saltwater, leading to a decrease in pH and an increase in acidity. Studies have revealed that ocean acidification induces fragility in the shells of oysters and adversely impacts their immune response [67–69]. When their immune responses are compromised, they become susceptible to diverse diseases, encompassing bacterial and parasitic infections [70].

As earlier stated, the vulnerability of oysters to several diseases can increase when their shells and immune systems are compromised. Carbonate chemical composition and pH changes can directly increase pathogenic infection, modulating microbiota and thus affecting the growth, redox state, and fertility of oysters.

For instance, Dermo disease, caused by the parasitic protozoan *Perkinsus marinus*, is highly destructive to oysters. According to [71], the exposure of Eastern oysters (*Crassostrea virginica*) to increased levels of CO_2 resulted in a notable increase in both infection rates and mortality. Furthermore, the vulnerability of oysters to parasitic infections in acidic environments could be due to the attenuation of oyster shells and immunological responses, along with modifications in the virulence and transmission rates of the parasite [20,28]. Recently, the alteration in secretory activity in mantle edge cells of Pacific oysters was verified, suggesting that the foliated shell layer might be the first compromised due to ocean acidification [72]. In Eastern oysters, increased levels of CO_2 had a significant impact on the incidence of *Vibrio* infections. Seawater pH and carbonate chemistry changes also impacted *Vibrio* bacteria growth rate and pathogenicity [73].

Thus, it is crucial to establish management practices that consider the possible effects of ocean acidification from climate change to support the expansion and survival of oyster populations. Addressing this issue is crucial, given the ongoing effects of climate change on ocean acidification. Additionally, in order to increase our comprehension of how ocean acidification affects oyster communities and find workable management strategies, extensive research and monitoring efforts may be required.

4. Climate Change and Oyster Diseases

Climate change is currently considered the most pressing environmental issue of our time (Figure 3), and it has had a notable and far-reaching impact on marine ecosystems [74]. The impact of climate change on marine ecosystems is complex and multifaceted, encompassing a diverse range of interrelated factors that impact the well-being and adaptability of these ecosystems [74,75]. Due to the absorption of a considerable amount of excess heat and carbon dioxide by the oceans from the atmosphere, many complexes and often unanticipated alterations are transpiring, affecting marine organisms [76]. Moreover, alterations in oceanic temperature and acidity can impact the abundance and dispersion of plankton, which serves as the fundamental building blocks of the marine trophic system [77,78].

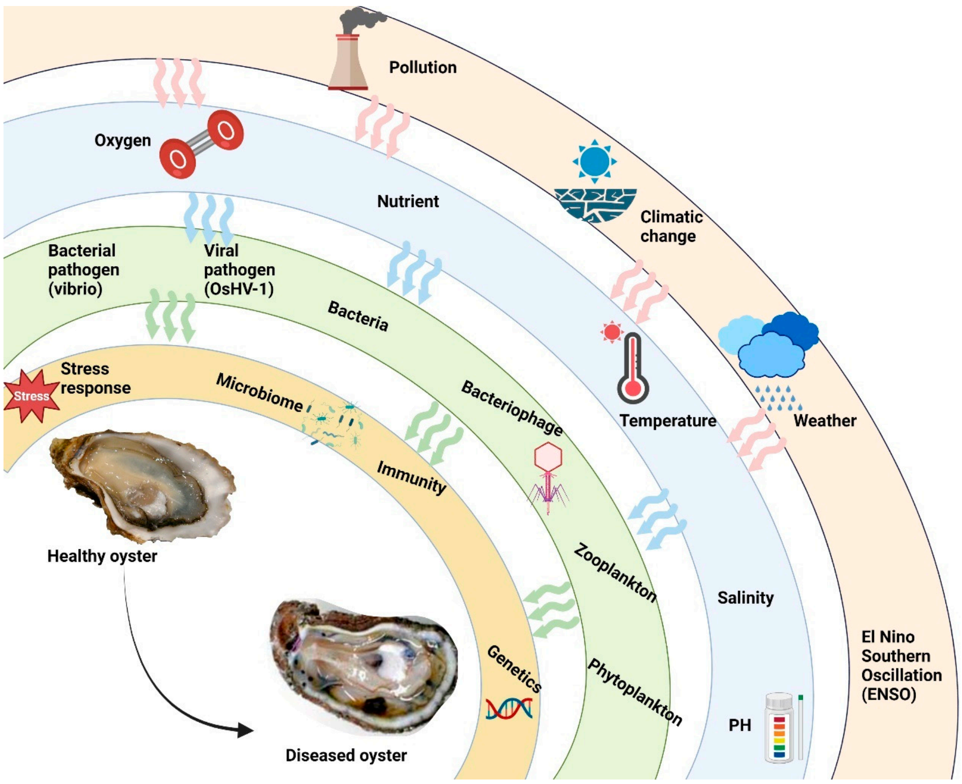

Figure 3. The interactome/synergism of oyster diseases. The outer rings are large-scale environmental events (e.g., climate change) that influence the lower rings (e.g., temperature), allowing for a cascade effect that eventually influences microbial communities and pathogens (e.g., increased pathogen proliferation) that can then act on the host, oysters.

Climate change significantly influences the susceptibility of aquatic organisms to fluctuations in water temperature, water acidity, and nutrient concentrations [19,79]. Thus, assessing the potential effects of climate change on marine ecosystems necessitates the consideration of this diverse range of environmental factors [80]. As earlier highlighted, one of the major impacts of climate change on marine ecosystems is the increased vulnerability of oysters to diseases.

Oysters function as filter feeders, thereby performing a crucial function in maintaining the quality of the aquatic environment. Filter feeders are crucial in maintaining water quality and serve as a significant source of sustenance and income for diverse societies [81,82]. However, they exhibit a high degree of sensitivity to fluctuations in the temperature and acidity levels of the water. For example, higher temperatures of over 20 °C encourage the growth and virulence of pathogens, while lower salinity levels decrease oysters' ability to resist infection [28]. Also, ocean acidification and warming adversely affect oyster growth rates and survival [83]. The potential consequences of this effect could be significant for both wild and cultured oyster populations. A summary of the impacts of climate variables on oysters resulting in diseases and mortalities is presented in Tables 1–4.

Table 1. Impacts of climate variables on different oyster species leading to diseases, their severity and spread.

Location	Species	Water Type	Parameters	Impact	Remark	References
China	N/A	N/A	Temperature, pH, sea level	Disease	*Vibrio parahaemolyticus*	[84]
USA	N/A		*Vibrio* spp.	Disease	*Vibrio* spp. abundance may increase with increasing temperature	[85]
USA	Eastern oyster (*Crassostrea virginica*)	Freshwater	Temperature	Disease	Dermo disease	[86]
N/A	Eastern oyster (*Crassostrea virginica*)	N/A	*Perkinsus marinus*	Disease	Dermo disease	[87]
USA	Eastern oyster (*Crassostrea virginica*)	Marine	Temperature, parasites	Disease	High-temperature adaptation of *P. marinus* strains	[79]
USA	Eastern oyster (*Crassostrea virginica*)	Freshwater	Protozoan pathogen, *Haplosporidium nelson*	Disease	MSX (multinucleated spore unknown) disease	[88]
Netherlands	Pacific oyster (*Crassostrea gigas*)	Marine	Temperature, parasitic infections	Disease	-	[89]
USA	Eastern oyster (*Crassostrea virginica*)	Freshwater	Parasite *Perkinsus marinus*	Disease severity	Dermo disease	[90]
Mexico	Eastern oysters (*Crassostrea virginica*)	Marine	Temperature, salinity	Disease severity	Dermo disease	[91,92]
USA	Eastern oyster (*Crassostrea virginica*)	Freshwater	Temperature, salinity	Disease prevalence	-	[93]
USA	Eastern oyster (*Crassostrea virginica*)	-	Temperature	Disease prevalence	Dermo disease	[94]
USA	Eastern oyster (*Crassostrea virginica*)	Marine	Salinity	Disease prevalence, mortality	Up to 100% prevalence of Dermo at some sites	[95]

Table 2. Impacts of climate variables on different oyster species leading to mortalities.

Location	Species	Water Type	Parameters	Impact	Remark	References
Australia	Pacific oyster (*Crassostrea gigas*)	Marine	pH	Mortality, stress	Reduced nitric oxide synthase and superoxide dismutase activities, lowered survival (33.5%)	[96]
France	Pacific oyster (*Crassostrea gigas*)	Marine	Temperature, chlorophyll	Mortalities	-	[97]
Australia	Sydney rock oyster (*Saccostrea glomerata*)	Marine	Temperature	Mortalities	A 12% higher mortality in selectively bred than in wild-type	[98]
USA	Eastern oyster (*Crassostrea virginica*)	Freshwater	Temperature, salinity, *Perkinsus marinus*	Mortalities	Above 36% in epizootic years	[99]
Australia	Pacific oyster (*Crassostrea gigas*)	Marine	Temperature	Mortalities	Spatial location is a significant determinant	[28]
USA	Apalachicola oysters	Freshwater	Salinity, drought	Mortalities	Mortality was size-specific	[57]
North South Wales	Sydney rock oyster (*Saccostrea glomerata*)	Freshwater	pH	Mortalities	However, resilience to acidification was exhibited	[59]
Australia	Pacific oyster (*Crassostrea gigas*)	Marine	Temperature	Mortalities	Mortality rate up to 77.4%	[100]
Canada	Pacific oyster (*Crassostrea gigas*)	Marine	pH, *Vibrio harveyi*	Mortalities	Bigger larvae usually fare better in corrosive saltwater	[101]
Italy	Pacific oyster (*Crassostrea gigas*)	Marine	Diverse pathogens, including *Vibrio splendidus* and *Vibrio aestuarianus*	Mortalities	Varied	[102]
USA	Eastern oyster (*Crassostrea virginica*)	Freshwater	Salinity, *Haplosporidium nelsoni*, *Perkinsus marinus*	Mortalities	Resilience in the population	[103]
France	Pacific oyster (*Crassostrea gigas*)	Freshwater	Temperature	Mortalities	Mortality up to 85%	[104]

Table 3. Impacts of climate variables on different oyster species leading to increased susceptibility to diseases.

Location	Species	Water Type	Parameters	Impact	Remark	References
Italy	Pacific oyster (*Crassostrea gigas*)	Freshwater, Marine	*Vibrio para-haemolyticus*	Susceptibility	Virulence factors in a few strains	[105]
Australia	Sydney rock oyster (*Saccostrea glomerata*)	Marine	pCO_2 and temperature	Susceptibility	Altered microbiome	[47]
Australia	Sydney rock oyster (*Saccostrea glomerata*)	Marine	CO_2 stress	Susceptibility	-	[54]
Spain	European flat oyster (*Ostrea edulis*)	Marine	Temperature, ocean acidification	Susceptibility	A bottleneck in pediveligers from 22 to 30 °C	[106]
UK	Pacific oyster (*Magallana gigas*) and native flat oyster (*Ostrea edulis*)	Marine	pCO_2, temperature	Susceptibility	A 40% *M. gigas* decrease at 750 ppm pCO_2	[60]
Mexico	American oyster (*Crassostrea virginica*)	Marine	Temperature, anthropogenic contaminants	Susceptibility	Prone to waterborne pathogen pollution	[107]
USA	Eastern oyster (*Crassostrea virginica*)	Marine	Temperature, parasitic infections	Susceptibility	Survival declined with increasing temperature	[108]
Mexico	Qyster (*Crassostrea corteziensis*)	Marine	Salinity	Susceptibility	Increased susceptibility but survival maintained above 96%	[109]
Mexico	Eastern oyster (*Crassostrea virginica*)	-	Temperature, tidal elevation, *Perkinsus marinus*	Susceptibility	Combined effects (biotic and abiotic factors and multiple parasites) on Dermo disease	[110]

Table 4. Impacts of climate variables on growth, immunity and metabolism of different oyster species.

Location	Species	Water Type	Parameters	Impact	Remark	References
USA	Pacific oyster (*Crassostrea gigas*)	Marine	pH	Growth, survival, immunity	Altered microbiome and reduced survival	[36]
USA	Pacific oyster (*Crassostrea gigas*)	Marine	pCO_2, pH	Growth	-	[111]
USA	Eastern oyster (*Crassostrea virginica*)	Freshwater	Salinity	Growth, survival	A trade-off between oyster growth and vulnerability to disease, increased mortality	[112]
China	Pacific oyster (*Crassostrea gigas*)	Marine	pH and long-term CO_2 exposure	Metabolism	Common response mechanisms in metabolism to short and long-term CO_2 exposure	[35]
China	Pacific oyster (*Crassostrea gigas*)	Marine	pCO_2	Immune response	Enzyme activity, increased apoptosis, and mRNA expressions	[34,70]

5. Temperature-Induced Oyster Diseases

Temperature plays a crucial role in the growth and development of oysters. Warmer temperatures can accelerate their growth rates, while cooler temperatures can slow them down. Temperature influences oyster metabolism, with higher temperatures generally increasing metabolic rates [113]. As a result, oysters may need more food to sustain their energy needs in warmer conditions. Changes in energy allocation can impact their overall health and resilience to stressors. Oysters have specific temperature tolerance ranges, and when the temperature goes beyond these ranges, it can lead to stress and even mortality [114–116]. Exposure to high temperatures for an extended period can result in heat stress, decreased immune function, and a higher susceptibility to diseases and pathogens [117,118]. On the other hand, oysters can become susceptible to freezing or low-temperature stress when exposed to low temperatures, resulting in disease and disease-induced mortality [117].

The water temperature greatly influences the growth and spread of oyster parasites. Warmer shallow waters, more so than colder deeper waters, offer better conditions for developing and reproducing oyster parasites like *Perkinsus marinus* and *Haplosporidium nelson* [119,120]. The protozoan parasite *Perkinsus marinus* causes a severe disease in oysters known as Dermo, which can result in high mortality rates [121]. Specifically, oyster parasites are frequently more concentrated in shallow water due to poor water circulation and increased nutrient concentrations, which may increase the possibility of infection and transmission among oysters [122]. Also, various stressors may be present for oysters developing in shallow waters, including temperature changes, low dissolved oxygen levels, and pollution exposure [123]. Consequently, the oysters' immune systems may weaken [51], thus rendering them more vulnerable to diseases. In addition, shallow-water oyster-growing sites usually have higher oyster population densities, which can increase disease transmission risk. Hence, diseases can transmit swiftly from one oyster to another by direct touch or floating freely in the water. To limit the risk of disease transmission, oyster growers can improve water quality, reduce oyster density, and monitor for signs of diseases [74].

Disease and disease-induced mortality patterns have been observed in *C. virginica*, attributed to climate variations from the El Niño-Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO). Elevated temperatures observed during the positive phase of the (NAO) facilitate the proliferation of parasites, thereby contributing to an increase in the mortality rate of oysters [99]. Salinity primarily regulates the disease process in *C. virginica* populations, as observed along the coast of the Gulf of Mexico [99]. In contrast, temperature primarily regulates the disease process, such as along the United States eastern seaboard coast. This suggests that oysters' responses toward alterations in a particular area's climate may not be a reliable predictor of how they might respond across a species' range [99]. Evidence shows that *P. marinus* can survive in environments with low temperatures and salinities [124,125]. Various factors, such as elevated winter temperatures, shallower water levels, and high densities of both hosts and parasites in oyster farms, contribute to the high infection rates of *P. marinus* [90]. The occurrence rates of *P. marinus* in certain areas may decline due to colder winters and increased precipitation, despite the species' ability to withstand low temperatures and salinities. However, if climate change models prove accurate and temperatures increase, epizootic conditions could emerge, leading to species resurgence [90]. There is a correlation between the emergence of a new, highly virulent phenotype of *P. marinus* and the increase in the incidence and severity of the disease and its associated mortality [126]. In Eastern oysters, one phenotypic alteration is a decrease in the parasite's life cycle duration, alongside a shift in their tropism from superficial connective tissues to digestive epithelia. Pathogen ranges are also expanding as ocean temperatures rise. One significant example is the northward spread of oyster infections in the mid-1980s [86,94]. During a winter warming trend in which the winter cold-water barrier to pathogen growth was eliminated, the eastern oyster disease (*Perkinsus marinus*) on the east coast of the United States further expanded its range from Long Island to Maine [127]. Over the years, there is a possibility that *P. marinus* has undergone adaptive modifications to cope with the reduced oyster population and lifespan. This suggests that the invasion of a marine parasite has elicited a unique response from the ecosystem, characterized by an increase in the virulence of a native parasite [126].

There appears to be a positive correlation between the increase in sea surface temperature and the proliferation of *Escherichia coli* bacteria in American oysters [107]. Laboratory-based heat exposure revealed that *E. coli* protein and mRNA expression in the digestive glands and gills increased when subjected to temperatures of 28 and 32 °C compared to 24 °C [107]. This suggests that oysters may be vulnerable to contamination by waterborne pathogens [107]. Elevated water temperatures can cause the proliferation of bacteria, like *E. coli*, leading to increased *E. coli* concentration in the water. Oysters are filter feeders and can accumulate *E. coli* in their tissues, and higher sea surface temperatures can make oysters more susceptible to bacterial infections.

One of the processes contributing to the increased severity of infection is the exposure of intertidal oysters to higher temperatures throughout the summer when air temperatures are much higher than water temperatures [108]. Oysters' survival rate decreased as the temperature increased, sharply declining between 39 and 43 °C. A rise in the average summer air temperature of at least 35 °C could directly impact oyster survival in the short term due to temperature-related effects and a long-term indirect impact due to the increased intensity of *P. marinus* infection [108]. The surrounding environment determines the body temperature of oysters, and they are well adapted to a specific temperature range, varying depending on the species and location. Their physiological processes can be negatively affected if the temperature rises beyond the optimal range [117]. A temperature rise can increase their metabolic rate, requiring more oxygen, which can be difficult to obtain because warmer water holds less dissolved oxygen. This can cause stress and reduced growth rates.

Additionally, a prolonged heatwave can make the water more acidic, damaging oyster shells and making them more vulnerable to predators [128]. If the average summer air temperature rises above 35 °C or less than 10 °C, oyster survival could be directly impacted, reducing growth rates, increasing stress levels, and making them susceptible to diseases and predators [18], possibly increasing the morbidity in the oyster population. This could lead to significant declines in oyster populations and the broader ecosystem that depends on them.

Research has demonstrated that the incidence of *P. marinus* is correlated with temperature and salinity, whereby reduced temperatures and salinities are generally associated with a lower likelihood of infection [88]. Sea surface temperature data support the hypothesis that rising winter water temperatures can significantly influence *P. marinus* epizootic outbreaks [86]. Elevated winter water temperatures can significantly impact the outbreak of *P. marinus*, which becomes more suitable for the reproduction and infection of oysters [79]. During winter, oysters are in a dormant state, making them more prone to infections from *P. marinus*. If water temperatures exceed a certain threshold, the parasite can proliferate faster, and the infection can spread quickly among oyster populations. Increased water temperatures can also affect their immune response, making them more vulnerable to *P. marinus* infections. Increased seawater temperature (e.g., from 20 °C to 25 °C) can result in a high mortality rate in oysters [100]. This highlights the adverse impact of marine heat waves on aquaculture-based food production. Temperatures rising can augment the probability of pathogen generation, endurance, and the likelihood of disease dissemination and host susceptibility.

Climate change is expected to increase disease impacts in most host–parasite systems. However, there is a possibility that a particular group of pathogens may decline due to warming, thereby releasing hosts from the risk of disease, including oyster pathogens [129]. Oysters are temperature-sensitive, and temperature changes can alter their development, reproduction, and immunological responses [117]. Furthermore, tidal patterns influence their ability to obtain nutrients and oxygen from the water, as high tides can bring in fresh, nutrient-rich water. In contrast, low tides can expose oysters to air and sediment [130,131]. For example, different stone pavers (white, grey, and black) attached to Pacific oysters (*Crassostrea gigas*) showed mean maximum substrate temperatures of around 34, 37, and 40 °C, respectively, at the lowest tidal point [98,132]. Across all pavers, wild-type oysters had 12% lower mortality rates than selectively bred oysters, although there were no statistically significant differences [98]. Regardless of whether or not the oysters are wild-type or selectively bred, there is currently no noticeable variation in the expression patterns of the various oyster populations on cold pavers [98].

Genetic clusters associated with *Vibrio parahaemolyticus* can be affected by temperature selection at temperatures below 15 °C or over 16 °C [105]. At 30 °C, European flat oyster (*Ostrea edulis*) larvae mortality rate can increase. No indication of bacterial adaptation to low-temperature environments was observed, as the net growth rates of isolates from different geographic sites showed similarity within the temperature range of 5 to 20 °C. Also, isolates exhibited differences in proliferation rates at different temperatures, suggesting parasite strains habitually exposed to higher temperatures may have developed adaptations to thrive in such conditions [105].

The relationship between temperature and diseases in oysters is complex, as other environmental elements can also influence oyster disease. Temperature influences the incidence and severity of oyster disease, a crucial environmental determinant [70]. Oysters are vulnerable to low temperatures, although it is more probable for higher temperatures to promote the proliferation and propagation of diseases [18,117]. Moreover, the impact of temperature on the proliferation and viability of oysters can influence their vulnerability to infections. According to [118], oysters may experience stress and mortality due to low winter temperatures. This condition could lead to a weakened immune system and increased susceptibility to infections in the following season. The impact of temperature on oyster diseases can manifest in various ways. For example, lower temperatures can slow infection development and reproduction, whereas higher temperatures can hasten these processes [117].

In Eastern oysters, the growth rate of the pathogen *Perkinsus marinus*, which causes Dermo disease in oysters, was more significant at temperatures ranging from 20 to 25 °C than at lower temperatures. One study observed the highest prevalence of the disease within the range of water temperatures spanning from 20 to 25 °C [126]. Also, *Haplosporidium nelsoni*, which causes MSX disease in oysters, exhibits a greater prevalence and intensity at elevated temperatures [88]. The MSX disease in oysters exhibits the highest prevalence and intensity at water temperatures exceeding 20 °C [99]. In the Gulf of Mexico, [133] revealed a significant correlation between the prevalence of MSX disease in oysters and the water temperature and nutrient availability. In addition, previous studies have indicated that temperature can influence the frequency and intensity of other oyster diseases, including QPX disease [134] and *Roseovarius crassostreae* infection [135]. Thus, future temperature changes could considerably impact the health of oyster populations by altering the frequency and severity of oyster diseases. Warmer temperatures, which can promote the growth of pathogenic bacteria in oysters, can exacerbate different disease conditions. Warm water, for instance, promotes the growth of *Vibrio* bacteria [136], which are responsible for different oyster diseases, including vibriosis and shellfish poisoning. As temperatures rise, the likelihood of *Vibrio* outbreaks occurring and the severity of these outbreaks are likely to rise, which is a major threat to oyster populations. Due to the complexity of the relationship between temperature and oyster diseases, it is imperative to consider a diverse range of environmental factors while assessing the impacts across different environmental conditions and localities.

6. Salinity-Induced Oyster Diseases

There are multiple ways in which climate change can impact the frequency and intensity of salinity events. Rising sea levels can also result in more saltwater infiltrating coastal aquifers [137], which may cause an increase in groundwater salinity. Furthermore, climate change can indirectly influence salinity levels by affecting other factors contributing to salinization, such as agricultural practices and land use changes. Several aquaculture species, such as the Pacific oyster (*Crassostrea gigas*), have demonstrated a significant relationship between increasing salinity and disease incidence. In Cortex oysters (*Crassostrea corteziensis*), the resistance when exposed to increased salinity (35 and 50 psu) was lower than that of oysters exposed to a decreased salinity [70,109]. This suggests that oysters are more prone to diseases, especially as salinity increases. As a result, this circumstance may increase their vulnerability to other environmental stresses, such as temperature and/or acidity, and their susceptibility to opportunistic pathogenic bacteria, which cause the most common oyster diseases [109]. Hypersaline conditions can affect oysters in various ways, both positively and negatively. Environmental factors, including salinity levels, play a crucial role in determining the severity of the disease. Research has indicated that high salinity levels can exacerbate Dermo outbreaks in oysters, resulting in significant economic losses for the shellfish industry. For example, the Cortex oyster is particularly sensitive to hypersaline conditions, which may increase vulnerability to environmental stressors like temperature and acidification. Furthermore, these conditions can also increase the oyster's susceptibility to opportunistic pathogens, which are the primary cause of oyster diseases [109].

7. pH-Induced Oyster Diseases

Changes in water chemistry can affect oysters, especially in terms of pH levels. An increasing or decreasing water pH can result in disease outbreaks [30], especially when it becomes too acidic or alkaline (and may cause weakened oyster shells). These oysters become more vulnerable to infectious pathogens, leading to high mortality rates. In acidic waters, Dermo disease and juvenile oyster disease (JOD) are two common examples affecting oysters in such environments [28]. *Vibrio tubiashii* causes JOD, which affects oysters below one year of age, while *Perkinsus marinus*, a protozoan parasite, causes Dermo disease, known for its fatal impact on oysters. Additionally, changes in the pH level can have a broader effect on oysters' health and survival by impairing their capacity to grow and reproduce, resulting in a potential reduction in oyster numbers [138]. For instance, Pacific oysters are particularly at risk due to lower survival rates during simulated marine heatwaves and *Vibrio* [36]. This indicates that soda ash's pH buffering mechanism during the initial stages of development may compromise life stages by altering the microbiota and diminishing the immune capacity during stressful conditions [36]. Thus, there is a need to adopt a long-term perspective on hatchery husbandry methods and mitigate climate change.

In addition, reducing pH levels in seawater due to increased acidity can significantly lower bacterial pathogenicity, particularly *Vibrio* spp. in *O. edulis* larvae [106]. Hence, seawater acidity can significantly impact the ability of bacterial pathogens to survive. Bacterial pathogens typically do best in a narrow pH range, and when the pH of seawater drops, it becomes more acidic, creating an inhospitable environment for many of these pathogens. The pH level of an aquatic environment significantly impacts the survival and pathogenicity of *V. cholerae* and *V. parahaemolyticus*. These two bacteria are most successful in environments with a pH level of 7.0–7.5, and their effectiveness decreases as the pH level drops. Bacterial cell membranes and enzymes are also at risk of being damaged by acidic seawater, reducing the bacteria's ability to cause harm [139–141].

8. Management Strategies for Oyster Diseases in the Face of Climate Change

Due to the impacts of climate change, oyster diseases are becoming more deadly and prevalent [142]. Thus, it is essential to implement effective management techniques that reduce their negative effects on the environment and business [56].

Several management strategies have been developed to lessen the effects of oyster diseases. Using oyster strains resistant to disease is one of the best methods. Incorporating oyster strains that are resistant to diseases offers various environmental advantages. For instance, oysters contribute to maintaining the balance of marine ecosystems [46]. Introducing disease-resistant oyster strains can prevent or reduce disease-related mortalities, thus ensuring a stable oyster population. This population stability may contribute to water filtration and higher water quality, ultimately benefiting the environment. This approach can also serve as a measure to prevent potential outbreaks, reducing the need for chemical treatments or antibiotics that may adversely affect the environment. In addition, integrating disease strains into oyster populations plays a role in preserving the genetic diversity required for long-term survival.

One example of successful efforts to address oyster diseases is the development of Eastern oyster breeds resistant to Dermo [124,143]. According to [144], using MSX-resistant oyster breeds has reduced the prevalence of MSX in oyster populations. Both methods indicate the potential advantages of selecting for disease resistance in oyster breeding. Probiotics also offer an alternate strategy for maintaining oyster health and lowering their risk of infection. Probiotics may strengthen invertebrates' immune systems, increasing their chances of survival and reducing the severity of diseases [145,146]. This highlights the potential of probiotics as a practical management strategy for maintaining oyster health [147]. Environmental conditions and water quality can also be monitored to predict *Vibrio* outbreaks. This can allow farmers to change hatchery water sources or remove oysters from the area until the bloom passes [28]. For many years, multiple authors have suggested that genetic enhancement for disease resistance to pathogens is an attractive option to decrease their effects on oyster production. A well-written experiment examined the resistance of six *Bonamia ostreae* enzootic European flat oyster stains against the Rossmore line nominated for its greater resistance to the disease. Selection for resistance to *B. ostreae* in *Ostrea edulis* was evidenced by several authors [148–150]. Another report [151] observed a superior survival (37% for controls and 81% versus for lines) and fewer parasite infections (25% for controls and versus 0% for lines).

Moreover, during six consecutive generations of the Rossmore line infected with *B. ostreae* with survival (>75%), researchers found the prevalence of *B. ostreae* infection to be low [148]. This indicates that Rossmore could be more resistant to *B. ostreae.* In Australia, the survival efficiency of Sydney rock oyster (*Saccostrea Glomerata*) against *B. ostreae* infection was improved by 23% and 29% [149] after three and four generations of selection, respectively, after exposure to *B. roughleyi* for hot and cold periods. In France, [150] explored the resistance of *C. gigas* to *V. aestuarianus* in triploid and diploid siblings. They established inconsistent results that could, in part, be elucidated relative to various patterns of energy allocation in diploid and triploid Pacific oysters throughout the year. The possibly of using genetic biomarkers for improving multiple kinds of stress resistance in oysters was implemented [56,152]; however, there are still many explorations in the Pacific oyster genome, and our understanding of its unique tolerance mechanisms is incomplete and needs further clarification.

To tackle the impact of climate change on oyster diseases and enhance effectiveness, we can adopt an approach that incorporates a mix of regulations, industry standards, fishery guidelines, and optimizations with probability scores. The proposed framework may entail the following sequence of actions:

Laws and Regulations (Probability Score: High): Implement existing laws and regulations relating to oyster farming. These rules must prioritize preventing diseases, implementing biosecurity measures and preserving the environment.

Best Practices and Biosecurity Measures (Probability Score: High): Monitor the adoption of best practices in oyster farming to minimize the risk of diseases. This may involve selecting suitable sites, regular cleaning and sanitation, and strict adherence to quarantine procedures when introducing new oyster stock.

Collaboration and Knowledge Sharing (Probability Score: High): Facilitate collaboration between government agencies, researchers, and industry stakeholders to share knowledge and experiences related to disease management.

Fisheries Directives and Monitoring (Probability Score: Medium): Develop guidelines for fisheries that promote oyster farming methods and establish protocols for disease

monitoring and reporting by farmers. Establish comprehensive disease surveillance and monitoring system to detect and respond to disease outbreaks quickly.
Research and Development (Probability Score: Medium): Invest in research to understand the impact of climate change on oyster diseases and develop disease-resistant oyster strains through selective breeding or genetic engineering.
Training and Education (Probability Score: High): Provide training and educational programs for oyster farmers to increase awareness of disease management strategies and the importance of adhering to best practices.
Investment in Technology (Probability Score: Medium): Invest in technological advancements such as automated monitoring systems or remote sensing technologies to improve disease detection.
Insurance and Risk Management (Probability Score: Low): Encourage adopting insurance and risk management practices within the oyster farming industry to reduce financial losses associated with disease outbreaks.

Combining these strategies and optimizing their implementation could significantly improve the efficiency of managing oyster diseases. However, the exact extent of efficiency improvement would depend on various factors, such as the level of compliance with laws and best practices, the effectiveness of disease monitoring systems, the success of research efforts, and the willingness of stakeholders to collaborate. In addition, the effectiveness of each strategy may vary depending on regional factors, policy contexts, and the level of commitment from various stakeholders.

9. Conclusions and Future Directions

Oysters, a vital natural resource, serve as a significant source of sustenance for both humans and wildlife. However, climate change has substantially impacted oyster populations and their disease susceptibility.

This article has discussed various ways climate change affects oyster health, including the possible consequences for ecosystems and societies that rely on these valuable shellfish. Climate change is causing an increase in temperature, adversely affecting oyster production via modulating the microbiota, physiology, immunity and genetic alterations. Warmer waters allow harmful pathogens such as bacteria and viruses to grow and spread quickly, making oysters more vulnerable to diseases such as *vibriosis* and *dermo*, which can even cause mortality. Consequently, many regions have experienced a decline in oyster populations, and some oyster industries have even crumbled. Aside from the temperature, other climate variables also significantly impact oysters' well-being and health. For example, the changes in water salinity promoted by climate change can pressure oysters and make them more vulnerable to diseases.

Furthermore, the rise in sea levels and an increase in the frequency and intensity of storms can cause harm to the habitats of oysters and disrupt the complex ecological systems that maintain a thriving oyster population. Although there have been some studies on the influence of temperature on oyster diseases, there is still a need to understand the relationship between temperature and disease better. Future research should focus on understanding the mechanisms by which temperature affects various oyster pathogens and how different temperature regimes may impact oyster health. Although research on oyster diseases has focused mainly on the effects of warmer water temperatures, it is essential to consider further the interactive impact of ocean acidification with other variables. Further investigation is needed to understand how acidification affects oyster health and susceptibility to disease and how it interacts with other climate-related factors using omics tools. Oyster diseases are anticipated to have diverse consequences in different regions based on the local environment and distinct pathogens. Consequently, future research should examine regional differences in oyster disease dynamics and identify locations where oysters may be particularly vulnerable to climate change impacts.

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