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Review article

Climate change impacts on oyster aquaculture - Part I: Identification of key factors

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ABSTRACT

Oysters are enriched with high-quality protein and are widely known for their exquisite taste. The production of oysters plays an important role in the local economies of coastal communities in many countries, including Atlantic Canada, because of their high economic value. However, because of the changing climatic conditions in recent years, oyster aquaculture faces potentially negative impacts, such as increasing water acidification, rising water temperatures, high salinity, invasive species, algal blooms, and other environmental factors. Although a few isolated effects of climate change on oyster aquaculture have been reported in recent years, it is not well understood how climate change will affect oyster aquaculture from a systematic perspective. In the first part of this study, we present a systematic review of the impacts of climate change and some key environmental factors affecting oyster production on a global scale. The study also identifies knowledge gaps and challenges. In addition, we present key research directions that will facilitate future investigations.

1. Introduction

Oysters are highly preferred species in aquaculture because of their resilience to severe environmental conditions. However, they are susceptible to climate change and its induced hazards. Oysters are highly valued for their economic, cultural, nutritional, and ecological importance. With an estimated 9 billion people on the planet by 2050, oyster cultivation will guarantee food security (Shumway et al., 2003; Godfray and Charles, 2010). Over the past decades, the production of oysters has been steadily increasing and is expected to continue (FAO, 2019, 2023). They are regarded as both keystone species and ecosystem engineers in the aquatic environment (Gutiérrez et al., 2003; Han et al., 2017). Oysters engage in top-down and bottom-up interactions with their environments (Coen et al., 2007). However, the top-down control via filter-feeding could dramatically reduce phytoplankton populations (Cranford et al., 2003; Newell, 2004; Forsberg et al., 2017) potentially affecting oyster performance itself (Bacher et al., 2003; Strohmeier et al., 2005). Additionally, they also impact other filter-feeders and grazers (Kluger et al., 2017). They are crucial in controlling the depth of light penetration and the quality of the water because of their filtration activities (Petersen et al., 2016). Energy flow patterns from the pelagic environment to the benthos are altered by oysters. Oysters are widely distributed across the globe. For example, the eastern oyster (*Crassostrea virginica*) has a wide geographical and latitudinal distribution. They are found in the Gulf of St. Lawrence, the Caribbean, and the Gulf of Mexico according to Lazoski et al. (2011). Oysters are ectotherms and euryhaline, however, they thrive in shallow estuaries where water temperature varies seasonally between −1.5 °C and 22 °C.

At both the regional and global levels, there has been substantial research and review on how climate change will impact oyster aquaculture (Okon et al., 2023; Gabrielle et al., 2021). However, these studies focused on climate change impacts on oyster diseases and oyster-predator dynamics. Also, the study used increasing water temperature as a key factor to the susceptibility of disease and predator interaction in the oyster ecosystem. From the broader perspective, comprehensive research has been done regarding the potential impact of

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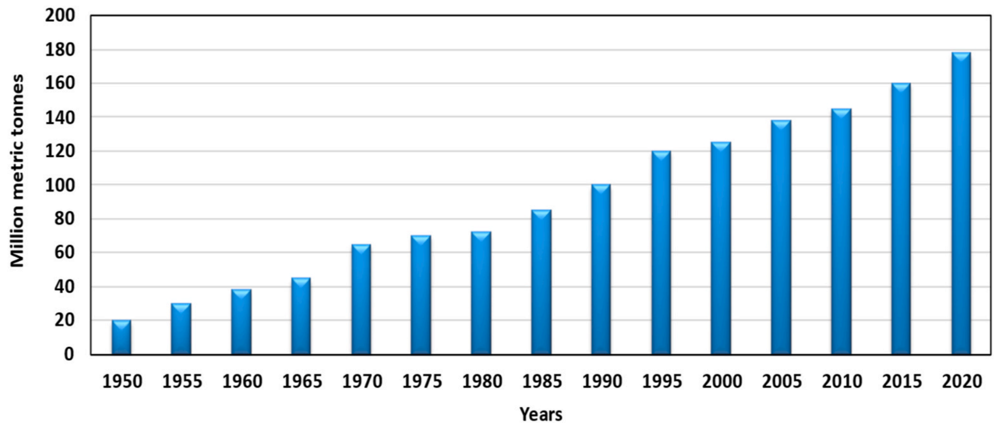


Fig. 1. Global aquaculture production from 1950 to 2020.
(Source: FAO, 2020).

climate change on aquaculture in general (De Silva and Soto, 2009; Bueno and Soto, 2017; Clements and Chopin, 2016; Yazdi and Shakouri, 2010; Chung et al., 2017; Froehlich et al., 2017; Handisyde et al., 2006; Harvey et al., 2017; Kluger et al., 2017; Dabbadie et al., 2018). Also, the present literature studies do not examine how climate change scenarios are utilized to forecast future oyster production. Therefore, this review is essential to promote producers' preparedness and help minimize the risks and impacts of climate change on oyster aquaculture. Such information is particularly helpful in determining the best climate change actions aimed at sustainable management of oyster resources.

Therefore, the objective of part 1 of this study is to systematically review and summarize (i) the impacts of climate change on oyster aquaculture production, and (ii) Identify key environmental factors affecting oyster production. More significantly, this review also identifies the research gaps, challenges, and future directions for the oyster aquaculture industry.

2. Global aquaculture and oyster production

2.1. Global aquaculture production

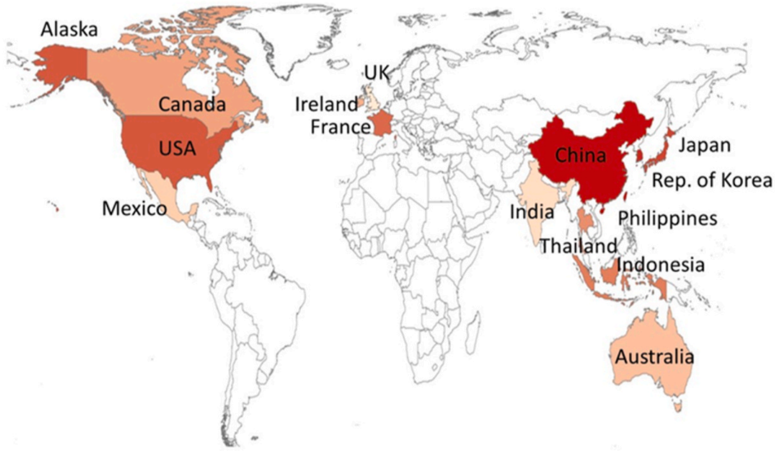
Globally, the aquaculture industry is expanding and now accounts for a larger portion of fisheries production. Asia and particularly China account for the majority of the world's aquaculture production. Aquaculture plays an important role in the livelihoods of people from diverse backgrounds. There are about 9.5 million aqua culturists in Asia and many more people will likely be involved in supplying a range of goods and services to the sector FAO (2020). Although the average rate of growth in the aquaculture sector appears to have slowed in recent years compared with the rapid growth seen during the 1980s and 1990s, continued expansion is predicted for the coming decades as a result of increasing demand for fish and the limited production capacity of capture fisheries. As a result of economic pressures and the increased development and spread of aquaculture technologies, it seems likely that a general trend towards more intensive cultural practices will occur. According to the FAO (2020), the total fisheries and aquaculture production have had a significant growth in the past seven decades going from 19 million tonnes (live weight equivalent) in 1950. This increased to a record of about 179 million tonnes in 2018. Additionally, the aquaculture sector expanded at a 3.3% annual rate. Aquaculture production declined marginally in 2019 (a fall of 1 % compared with 2018) but increased by a mere 0.2 % to reach 178 million tonnes in 2020. The total combined value of fisheries and aquaculture production in 2020 was estimated at USD 406 billion. However, aquaculture production alone had a value of USD 265 billion. Furthermore, the marginal decline since 2018 could be due to the impact of the novel COVID-19 as suggested by FAO (2020). Fig. 1 is an illustration of global aquaculture production from 1950 to 2020.

Table 1
Oyster species and their geographical distributions around the world.

Common Name	Scientific Name	Geographical Distribution
American cupped oyster	*Crassostrea virginica*	USA, Canada, Dominica Rep.
Pacific cupped oyster	*Crassostrea gigas*	China, Japan, Korea, Thailand, Australia, NZ, Malaysia, Canada, US, Mexico, France, Ireland, Netherlands, Channel Is., UK Spain, Portugal.
European flat oyster	*Ostrea edulis*	France, Ireland, Netherlands, UK, Spain, Portugal, Channel Islands.
Hooded oyster	*Saccostrea cuccullata*	Mauritius
Gasar cupped oyster	*Crassostrea gasar*	Senegal, Gambia
Cortez oyster	*Crassostrea corteziensis*	Mexico, Chile
Chilean flat oyster	*Ostrea chilensis*	Chile
Mangrove cupped oyster	*Crassostrea rhizophorae*	Cuba, Puerto Rico, Jamaica
Olympia oyster	*Ostreola conchaphilia*	USA
Indian backwater oyster	*Crassostrea madrasensis*	India, Sri Lanka
Slipper cupped oyster	*Crassostrea iredalei*	Philippines
Sydney rock oyster	*Saccostrea glomerata*	Australia
Portuguese oyster	*Crassostrea angulata*	Portugal
West African mangrove oyster	*Crassostrea tulipa*	West Africa (Ghana)

2.2. Global distribution of oyster species

Oysters are widely distributed and can be found throughout the world. In North America alone, there are at least 150 varieties of oysters. Globally, farmed oysters include over twelve different species both native and introduced as shown in Table 1. Most of the oyster species used in aquaculture farming can be found naturally in shallow depths in marine and brackish areas that are closer to the coast. In principle, oyster can close their shells during harsh environmental conditions. This includes changes in salinity and water temperature. Most critically, they become exposed during low tide when salinity declines. Their ability to adapt makes oysters a good species for aquaculture. More importantly, they can be farmed in locations that are accessible at low tide.



Country	MT - 2018
China	5,139,760
Korea	303,200
USA	153,909
France	84,910
Philippines	28,708
Indonesia	24,863
Thailand	21,048
Japan	17,600
Canada	14,614
Ireland	10,369
Australia	6,558
Mexico	6,305
India	4,000
UK	2,325

Fig. 2. Global oyster production (Metric tonnes) and key oyster-producing countries in 2018. (Source: FAO, 2019).

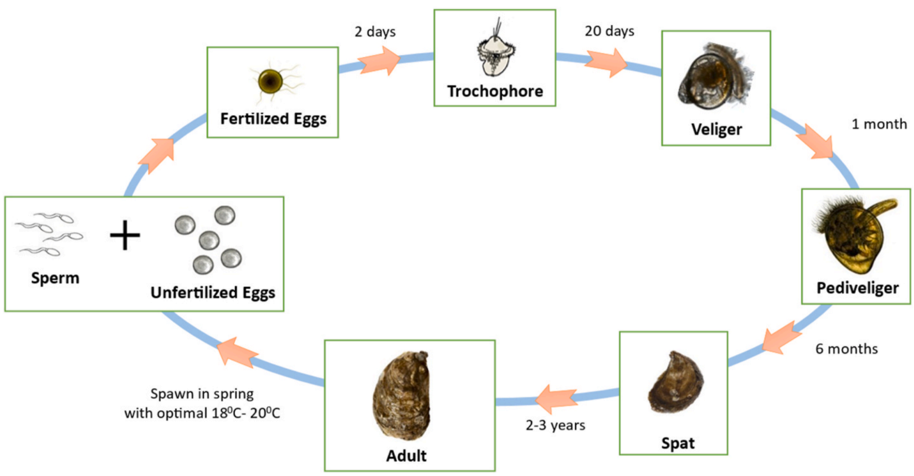


Fig. 3. The life cycle of oyster (*Crassostrea virginica*).

2.3. Global oyster aquaculture production

Since 1990, oyster aquaculture production has grown significantly, from 1.2 million tonnes to 6 million tonnes in 2018 with a value of US $7.46 billion. China consumes almost all of its production, accounting for about 85% of the world's oyster production (FAO, 2019). In addition, around 50,000 tonnes of oysters are traded annually on the global market. Countries like Korea, France, and China are major exporters of oysters. The top three EU nations for oyster imports are France, Spain, and Italy, although France is also one of the top exporters (FAO, 2019). Oysters have a relatively short shelf life, which hinders large-scale international trade because consumers frequently prefer live, in-shell oysters or freshly shucked meats. Furthermore, value-added and convenience products, including canned oysters and frozen or vacuum-packed oysters prepared with various sauces, can potentially be distributed globally. Fig. 2 shows the leading oyster-producing (Nations, 2018).

2.4. The life cycle of oyster species

The first stage of the oyster's life cycle begins when the gametes are fertilized and the cells divide into an embryo. It takes about 2 days to reach the trochophore stage. Then hair-like structures called "cilia" develop allowing it to move through the water column. It takes about 20 days to reach the d-hinge veliger stage. Then two shells ("bi-valves") and the "velum" an organ for movement and eating develop. The free-swimming larval oyster grows a foot (ped) after about 2–4 weeks and becomes ready to firmly attach itself to a hard surface, typically an old oyster shell, during the pediveliger stage. A spat develops once the pediveliger is firmly attached and begins to grow for about six months. From this permanent spot, the young spat filters algae from the water and grows quickly. After a few months, the spat grows to a size of about 5 mm long and 4 mm wide and reaches the juvenile stage. The oyster grows throughout the juvenile stage until it becomes an adult. Once the oyster reaches the adult stage, it can reproduce, and the life cycle continues in the next generation. However, the majority of oysters are male when they first reach adulthood and change to female as they age. Fig. 3 is an illustration of the life cycle of oyster species.

3. Environmental factors affecting oyster production

3.1. Effects of CO_2 and global percentage share of emissions

According to Maulu et al. (2021), the absorption and increasing amounts of anthropogenic activities that release CO_2 into the oceans and water bodies result in acidification. This has detrimental impacts on shell-forming aquatic life, especially oysters. Since the industrial revolution, there has been about a 26% increase in water acidity. However,

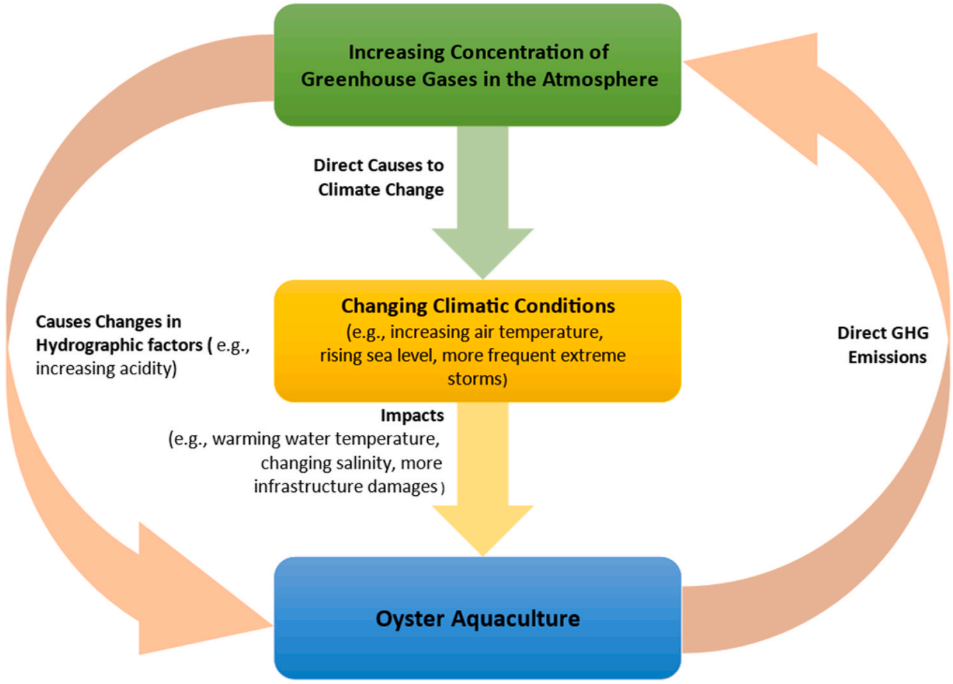


Fig. 4. Pathways through which climate change will affect oyster aquaculture.

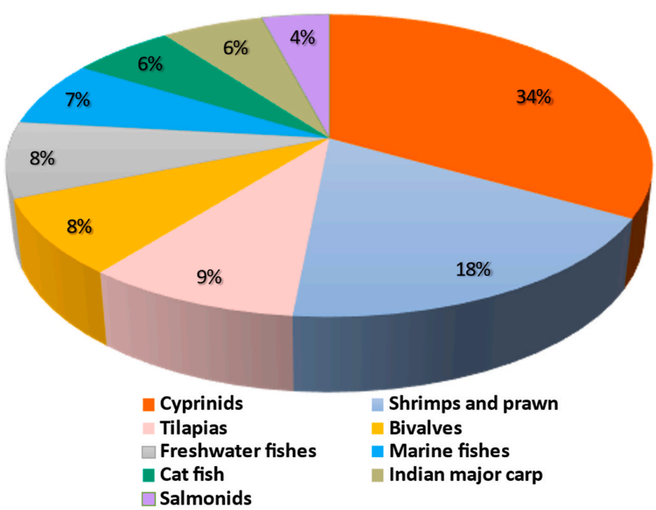


Fig. 5. Global percentage share of calculated CO_2 emissions by species in 2019. (Source: MacLeod et al., 2019).

this trend is expected to continue in warmer low and mid-latitudes (FAO, 2019). For about two decades, long-term dramatic decreases in ocean pH have been observed throughout the North Atlantic. In addition, it has been predicted that the pH of both oceans and water bodies is expected to decline further. In principle, this will affect commercial shellfish or the early life stages of cultured oyster species and this has a repercussion on their survival rate (FAO, 2019). The increasing acidity of coastal water bodies is a threat to oyster aquaculture. This is because the absorption of CO_2 and partial pressure of CO_2 (pCO_2) is higher in coastal waters than in the open ocean (FAO, 2019). The impacts of climate change on aquaculture production are both direct and indirect. The physical state and physiology of finfish and shellfish production systems are among the immediate effects. Additionally, indirect consequences could result from changes to input supplies, ecosystem structure, and secondary production. This may affect product prices, especially spat feed (formulated algae) as well as other goods and services needed by oyster farmers. Fig. 4 is an illustration of how increasing concentration of greenhouse gas (GHG) emissions in the atmosphere will impact on oyster culture production.

Although aquaculture activities, such as power input, transportation, and feed production are considered the main pathways of the sector's contribution to GHGs, its contribution is relatively minimal. This is because when compared to other food production sectors it is significantly less. For example, the effect of aquaculture on carbon dioxide and other global warming gas emissions in 2010 was estimated at 385 million tons. This was about 7 % of the agricultural sector's contribution that year (Maulu et al., 2021). Fig. 5 displays the global emissions disaggregated by species group. In addition, the geographical pattern of emissions closely mirrors production. Also, the aquaculture farm energy usage and N_2O emissions account for the majority of the non-feed emissions.

MacLeod et al., 2019, did a comprehensive analysis of CO_2 emission by specific species with a focus on a global perspective. His analysis was based on the total emissions disaggregated by species group, geographical region, and emission category.

The majority of emissions originated in the areas with the highest productivity (e.g., East Asia and South Asia). For the majority of species groups, emissions and production are also highly correlated, e.g., cyprinids are responsible for 34 % of emissions and 32 % of production. However, there are some exceptions. For instance, from the global perspective, shrimp account for 18 % of emissions but only 9 % of production, while bivalves produce 9 % of emissions but represent 23 % of production (Fig. 5).

3.2. *Global emission of aquatic N_2O*

Several factors are accounting for the increasing amount of N_2O gas in aquaculture systems. They include the type of feeding rate, water exchange rate, dissolved oxygen, pH, water temperature, etc. Microbial activities such as nitrification and denitrification on a fish farm result in N_2O emissions according to Hu et al. (2012). In principle, nitrous oxide (N_2O), stays in the atmosphere and is then converted to nitrogen oxide (NO_2) which in turn depletes the stratospheric ozone layer and exposes the earth to more solar radiation resulting in warmer temperatures.

However, it is challenging to quantify the emissions from the surface of a pond or estuary to the atmosphere. N_2O emissions from fish farms depend on pH and dissolved oxygen content and both fluctuate greatly (Bosma et al., 2011). For calculation purposes, Hu et al. (2012) included the N_2O emissions from ponds to illustrate their likely contribution to the total emissions, and to allow the comparison of the GHGs associated with aquaculture products. In their analysis, they were able to determine the amount of N_2O. This was done by multiplying the production by emission factor per kg of production (i.e., 1.69 gN_2O–N per kg of production, or 0.791 $kgCO_2e$/kgLW production). Furthermore, this is greater than the 0.71% utilized by Henriksson et al. (2014) in the calculation, which translates to a conversion rate of N to N_2O–N of 1.8 %.

3.3. Water temperature

The physiology, gene expression, distribution, as well as health of oysters, are influenced by water temperature (Zippay and Helmuth, 2012; Shelmerdine et al., 2017). The ectothermic nature of oysters makes their internal body temperature match that of external water temperatures. This is exceptional for intertidal species which are subject to aerial exposure. Although the effect of temperature on physiology is species-specific, generally, as water temperature increases, physiological rates will increase until a threshold is met, and this will eventually result in a performance decrease (Kooijman, 2010). The relationship between physiological functions such as dissolved oxygen consumption and filtration rates, and variations in temperature over short periods will inevitably affect how long they can survive (Malham et al., 2009). In addition, the long-term changes (years) will impact their reproductive timing and effort, and consequently their spatial distribution (Kittner and Riisgård, 2005; Filgueira et al., 2014). The impact of climate change and the relationship between water temperature and the physiology of oysters is very crucial. Most importantly, high-temperature intervals may favor the growth of aquatic species. This is more prevalent in temperate locations. Specifically, this will favor the production of warmer aquatic species, such as the giant tiger prawn, tilapia, oysters, and mussels (Pickering et al., 2011; Guyondet et al., 2018; Colden and Lipcius, 2015). Along with the increasing water temperature due to global warming, the IPCC et al. (2021) has predicted extreme climate phenomena such as heavy rains, heat waves, and droughts. Seasonal and interannual variations in water temperature and salinity caused by these occurrences will have a considerable impact on organism survival and behaviors in the aquatic ecosystem. Therefore, species inhabiting the coastal and intertidal areas, especially oysters, will be vulnerable to such changes. However, the stress induced by temperature and salinity fluctuations are distinct from each other (Woodin et al., 2020).

3.4. Sea level rise

Sea level rise will negatively impact oyster aquaculture breeding programs and the economic sustainability of the sector. The influx of saline water caused by sea level rise is projected to have an impact on aquaculture production infrastructure, including ponds, cages, and pens, especially in lowland areas (Kibria et al., 2017). Oyster aquaculture production and freshwater fisheries resources are known to be negatively impacted by salinization (Handisyde et al., 2006; Kibria et al., 2017). Additionally, changes in species composition, organism abundance and distribution, ecosystem productivity, and phenological shifts are likely to be brought on by sea level rise, particularly in farms located near estuaries. As a result, this could endanger the growth of cultured oysters in low-lying coastal areas (Doney et al., 2012). There are associated benefits with aquaculture activities that are social and environmental which are explored by coastal communities. However, these activities are directly and indirectly affected by rising sea levels, thereby endangering the production and sustainability of the sector. On the positive side, sea-level rise may increase the areas suitable for brackish water culture which are of high economic value species Handisyde et al. (2006); Kibria et al. (2017). In recent years, the sea level has increased by an average of 3.1 mm/year as a result of climatic and non-climatic factors (Dangendorf et al., 2017). The rate of increase varies greatly by region, with Western Pacific having values up to three times the global average and Eastern Pacific having values of either zero or negative. Over the past century from 1901 to 2010, the sea level rose by a global average of 0.19 m. It is projected that between 2000 and 2100, the global mean sea level rise (SLR) will very likely (90 % probability) reach between 0.5m and 1.2m under RCP8.5, 0.4m–0.9m. Furthermore, under RCP4.5, 0.3m–0.8m under RCP2.6 (Kopp et al., 2014).

3.5. Changes in precipitation patterns

Changes in rainfall patterns will affect oyster production and sustainability in two different ways. The increase in rainfall will cause flooding while low periods or no rainfall will eventually result in drought. According to the IPCC et al. (2018), risks resulting from drought events are likely to be higher at 2 °C compared with 1.5 °C of global warming in a given region, while flooding event patterns are difficult to predict with certainty. Studies have shown that increased patterns of rainfall, particularly in low-lying coastal areas will cause production risks in aquaculture farms (Bell et al., 2010). Some of the risks include losing cages during floods. Secondly, the invasion of cages by unwanted species. Thirdly, damage to cages and washing away (Rutkayova et al., 2017). The excessive influx of rainwater in oyster farms, especially those in the wild, could negatively affect environmental sustainability. Furthermore, this could also lead to water quality deterioration and high turbidity due to runoff. Additionally, losses from cages pose a challenge to the social and economic aspects of aquaculture sustainability by reducing the financial rewards for the farmers. However, drought may lead to water shortage and cause stress to oysters. Furthermore, this could lead to water quality deterioration and may have negative effects on aquaculture production (Hambal et al., 1994). Shortage of water through changes in the pattern of precipitation is likely to cause disputes among users especially those engaged in aquaculture, and agriculture, as well as domestic and industrial users (Handisyde et al., 2006; Barange et al., 2018).

3.6. Ice surface layer formation

Although, there is little scientific information on the effects of snow on oyster aquaculture. Ice surface layer formation in winter can be a serious threat to aquatic organisms especially those cultured in ponds, bays, and estuaries. Ice surface layers can inhibit the rate of photosynthesis and dissolved oxygen during the winter season. Furthermore, it may impede respiration of the aquatic organisms. Additionally, the ice surface layer depending on the depth can hinder the filter-feeding ability of oysters. Furthermore, it poses a significant threat to the life cycle of oysters. In principle, the mortality of cultured species is highly probable in such situations. At extremely low temperatures oysters may hibernate. This will result in retardation in growth and affect the quality of meat and the market price. Oysters living in their natural environment are more likely to be affected by the ice surface layer than those cultured. This is because cultivated oysters are more carefully controlled during their early life stages before they are released into farms. For instance, oyster farmers, particularly in Prince Edward Island (PEI), Canada lower their cages deeper in the water column in winter conditions when an ice surface layer is formed. Ice layers also increase production costs since, particularly in PEI, producers must use chainsaws to cut through the ice before they can harvest oysters in winter. Future research could therefore concentrate on the effects of snow ice on the life cycle of oysters.

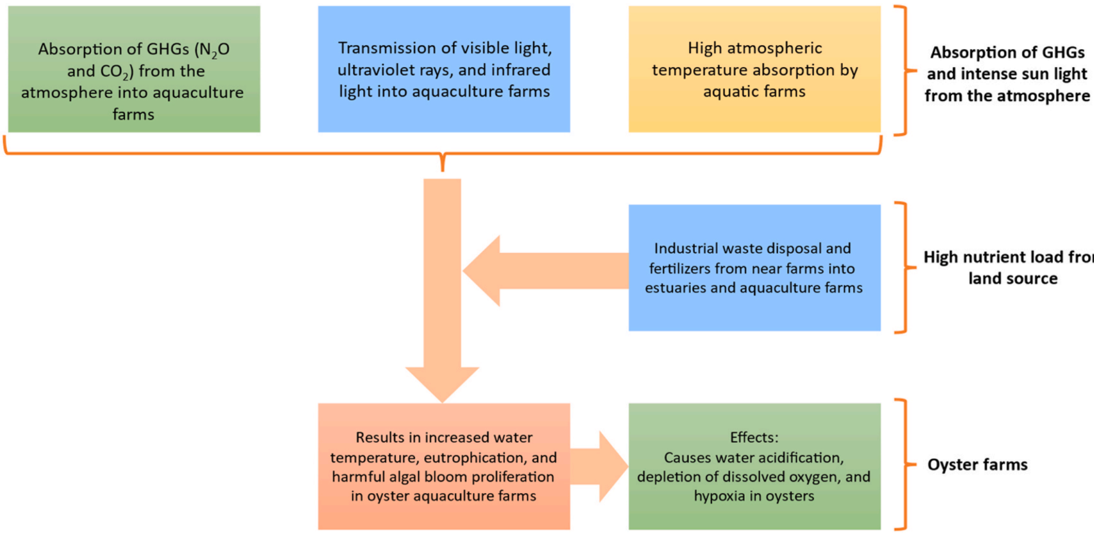


Fig. 6. The effects of GHG emissions (N_2O, CO_2) and other factors affecting oyster production.

3.7. Siltation and sedimentation

High levels of siltation are known to be deleterious, especially to eastern oysters (*Crassostrea virginica*), and the collective effect of suspended and bedded sediment is understudied from the perspective of oyster farming and bed restoration (Poirier et al., 2021). Sediments may cover the cages of oysters and prevent water flow through the cages. Oysters are ecosystem engineers, therefore the detrimental impacts of siltation on both larval and adult oysters may eventually have cascading repercussions on the surrounding biological population. Sediments from floods due to erosion and rains in aquaculture sites cause high turbidity. According to Carriker (1986), excessive amounts of suspended silt may negatively affect oyster larvae by interfering with their ability to feed. Additionally, oysters that live in turbid conditions in their natural habitats have developed a filtering system to distinguish inorganic particulates from food in suspension. Moreso, oysters reject inorganic particulates through the production of pseudofeces. Even though juvenile and adult oysters can survive under moderately turbid environments, the deposition of sediment may have a detrimental effect on the survival and development of oysters (Lenihan, 1999) and can prevent natural reef-building processes (Colden and Lipcius, 2015). In addition, the infilling of interstitial voids in the bed structure caused by increased sedimentation lowers the quality of the habitat. Most critically, oyster spat settlement rates can be lowered by sediment deposition. Additionally, Mackenzie (1983) showed that even a small amount of silt can prevent the substrate from being used for spat attachment. Increased sediment accumulation has the potential to bury some oyster cages partially or completely, creating dangerous hypoxic conditions and catastrophic oyster mortality (Colden and Lipcius, 2015).

3.8. Turbidity

According to Sandèn and Håkansson (1996), turbidity levels in water bodies are rising due to human activity in coastal areas. The total suspended particulate matter generally inhibits the growth of oysters by diluting the organic matter at high levels (Barange et al., 2018). Turbidity rarely exceeds aquatic organism tolerance levels relative to other abiotic factors like salinity, temperature, and dissolved oxygen. Instead, turbidity impairs predators' vision and changes top-down forcing (Liljendahl-Nurminen et al., 2008). In addition, the increasing nutrient input and erosion are the two primary sources of turbidity that are significantly influenced by human activities (Candolin et al., 2008); and cause siltation in lakes and streams (Khan and Ali, 2003). Moreso, it can decrease light penetration needed for photosynthesis. Therefore, decreasing food production and dissolved oxygen solubility to levels that are harmful to oyster populations. In principle, eutrophication is one of the primary causes of increased turbidity in marine environments (GESAMP, 1990). Turbidity also affects the ecosystems of oyster reefs by altering interactions between predators in the food web. According to (Lunt and Smee, 2014), it affects the distribution of mobile species and alters predation levels and the abundance of intermediate predators, which indirectly alters food webs. Turbidity is known to have an indirect effect on juvenile eastern oysters, an important ecosystem engineer in estuarine systems.

3.9. Salinity

Salinity is considered one of the most consequential environmental stressors for the culture of oysters along coastal areas (Miller et al., 2007; de Albuquerque, Ferreira, Salvador and Turini, 2012). Salinity is seen as a variable parameter reflecting the input of freshwater from precipitation, ice melting, river runoff, and loss of water through evaporation. Additionally, the mixing and circulation of surface water with underground water (Koblinsky et al., 2003; Cochrane et al., 2009). Evaporation is anticipated to increase with the increase in global temperatures, causing variations in water surface salinity. Rodrick (2008) reported that at lower salinity levels, oysters are susceptible to bacteria invasion. He further discovered that the differences in salinity may have an impact on oyster immunological function, specifically the capacity of hemocytes (blood cells) to resist foreign bacterial invasion.

In general, there is a prediction of high mortalities for several species including cultured oysters due to increased variation in water salinity. The result will be an adverse effect on the economic and social sustainability of the sector through increased loss of species and higher management costs. There is a need for future research to focus on the effect of salinity at levels lower than an optimal requirement on oyster aquaculture. However, few studies have been done on how various commercially significant species like oysters react to variations in salinity as a result of climate change. This scientific knowledge would be very useful for adaptation strategy for aquaculture, as changes in salinity may favor some species that are more saline tolerant (Jahan et al., 2019).

3.10. Algal blooms

The term "harmful algal blooms" (HABs) refers to naturally occurring accumulations of microscopic algae in water bodies. They are distributed worldwide and pose threats to the aquatic ecosystem. About 2% are known to be harmful. Blooms of harmful algae can have varied impacts on marine ecosystems, depending on suspension filter-feeding oysters who show size-selective feeding on phytoplankton. Therefore, algal bloom under thermal stimulation could be controlled. However, in oyster farming, this would cause the phytoplankton community to be altered. Both Marshall et al. (2009) and Li et al. (2015) reported that HABs occur more frequently in the mesohaline and polyhaline regions, most especially in major tributaries and estuaries in coastal regions. These same geographical areas, however, are particularly favorable for the growth of oyster reefs (Smith et al., 2005; Carnegie and Burreson, 2011). The U.S. government and shellfish growers from Maryland and Virginia together performed research and surveys in the mid-2000s, which revealed several needs for the shellfish sector. The establishment and maintenance of good water quality, specifically for the shellfish species being cultivated, was one of the most crucial and significant findings (Oesterling and Luckenbach, 2008). To adequately assess the hazards posed by algal blooms on aquaculture production, farmers need to utilize the use of technologies that would identify such occurrences and respond to them. Fig. 6 gives an illustration of the effects of GHG emissions (N_2O, CO_2) and other factors that contribute to the proliferation of algal blooms.

3.11. Dissolved oxygen

Dissolved oxygen (DO) is an important component of aquatic ecosystems. Changes in its content have a significant effect on the global nitrogen and carbon cycles (IPCC et al., 2014). The existence of bacteria, plants, fish, and other invertebrates depends on the presence of dissolved oxygen in the aquatic ecosystem. Excessive algal growth and decomposition result in low dissolved oxygen in the aquatic environment. Low DO is known to create physiological stress on oysters (Diaz and Rosenberg, 1995; Vaquer-Sunyer and Duarte, 2008) by impairing growth, reproduction, and immune functions, and reducing available habitat. Accordingly, low DO has been associated with the loss and unsuccessful rehabilitation of numerous oyster reefs (Cheney et al., 2001, Beck et al., 2011). Oysters can tolerate low DO conditions. In addition, the ephemeral and episodic nature of its low DO conditions (Breitburg, 1992; Johnson et al., 2009), makes it challenging to compare how low DO affects the growth and survival of oysters and other commercially important species (Hoback and Barnhart, 1996; Carmichael et al., 2004, Keppler et al., 2005). Furthermore, *C. virginica* can survive hypoxia ($<$1 mg/L) for 3 to $>$28 days (Stickle et al., 1989; Gray et al., 2002). The potential effects of low DO on oysters include changes in stress protein expressionPatterson et al., 2014, and reduced feeding, settlement, growth, and reproduction (Wallace et al., 2002). The improvement of fundamental knowledge of oyster physiology requires the detection of sub-lethal and cumulative effects of DO on oysters. This will also help with site selection for continuing restoration and management efforts ongoing worldwide (Beck et al., 2009; Schulte et al., 2009). Furthermore, understanding how low DO concentrations specifically affect oysters could provide an early physiological indicator of stress to avoid mortality.

3.12. Pathogens and diseases

The culture of oyster is associated with some pathogens, *Vibrio* species which are responsible for epidemics, and zoonoses (Austin, 2010; Le Roux et al., 2015). *Vibrio aestuarianus* strains as well as a group of the Splendidus clade have been linked to mortality in farmed oysters during the past two decades (Soletchnik et al., 1999; Gay et al., 2004; Lemire et al., 2015). *Vibrio aestuarianus* has also been identified as a serious pathogen for adult oysters (Travers et al., 2017), whilst *Vibrio tasmaniensis* and *Vibrio crassostreae* strains of the Splendidus clade are linked to a multifactorial sickness affecting spats and juveniles (Gay et al., 2004; de Lorgeril et al., 2018), which is triggered by the herpes virus (Segarra et al., 2010; Martenot et al., 2011). According to Pernet et al. (2014), this disease, also known as Pacific oyster mortality syndrome, appears during specific seasons when there is a drastic change in water temperatures from 16 °C to 24 °C. In oyster farms, mortality is seen in summer, especially on the French Atlantic coast, and in the spring and autumn on the Mediterranean coast, which is characterized by warmer seawater temperatures. The detection of virulence factors constitutes an essential part of the risk assessment for human pathogenic Vibrio species (Food and Agriculture Organization of the United Nations/World Health Organization (FAO/WHO), 2011), some of which have been identified in populations belonging to the Splendidus clade. In addition, the recent discovery of virulence factors in *V. tasmaniensis* and *V. crassostreae* has enabled more accurate monitoring of splendidus clade populations potentially pathogenic to oysters. Splendidus clade populations are potentially pathogenic to oysters. In addition, domoic acid, commonly known as Amnestic Shellfish Poison (ASP), is also produced by the diatom pseudo-nitzchia sp. Being microscopic algae, they cause diseases in oysters after ingestion. It further causes cardiovascular, instability seizures, and permanent short-term memory loss in humans. Table 2 shows some observed diseases and parasites of oyster species.

Table 2
Some observed diseases and parasites of oyster species (FAO, 2019).

Disease	Agent	Type	Syndrome	Measure
Denman Island Disease	*Mikrocytos mackini*	Protozoan parasite	None	Restricted modified culture practices
Nocardiosis	*Nocardia crassostreae*	Bacterium	None	Modified culture practices
Herpes-type virus disease of *C. gigas* larvae	None	Virus	None	None
Oyster velar virus disease (OVVD)	None	Virus	None	Unknown

3.13. Predation

Oyster aquaculture farmers have more control over predation depending on the design of their farms. The use of cages and longline culture protects them from predators. In some farms, oysters are protected from invertebrate predators using mesh sacks. In addition, the off-bottom culture technique elevates the oysters from the water column, preventing predators from having access to them. Additionally, oysters can be raised in hatcheries until they reach an appropriate size and become less vulnerable to predators before being transferred to farms (FAO, 2019). The physiological reactions of oysters to the changing environment could make them more vulnerable to predators. Oysters are very adaptive to their environment and can grow in a highly variable way depending on the conditions in the exact location. As a result of increased predator presence in the aquatic environment, the growth of individual species could be altered in response to defense (Lord and Whitlatch, 2012). Oyster spat are vulnerable to predation from starfishes, especially those cultured in bays and estuaries. Additionally, some of the major predators of oysters include fish species and invertebrates, such as crabs and snails. Many species respond to climate change by moving into different areas as the current habitat becomes unsuitable and new areas become preferable. Therefore, prey living in areas that provide habitat from predators will become more vulnerable as a result of the shift of predator species (Doney et al., 2012). Predators of oysters generally prefer a higher salinity environment. Therefore, increased estuary salinity which is driven by the decrease in river discharge may leave oysters without low-salinity refuge habitat (Kimbro et al., 2017). This may impair their capacity to protect themselves

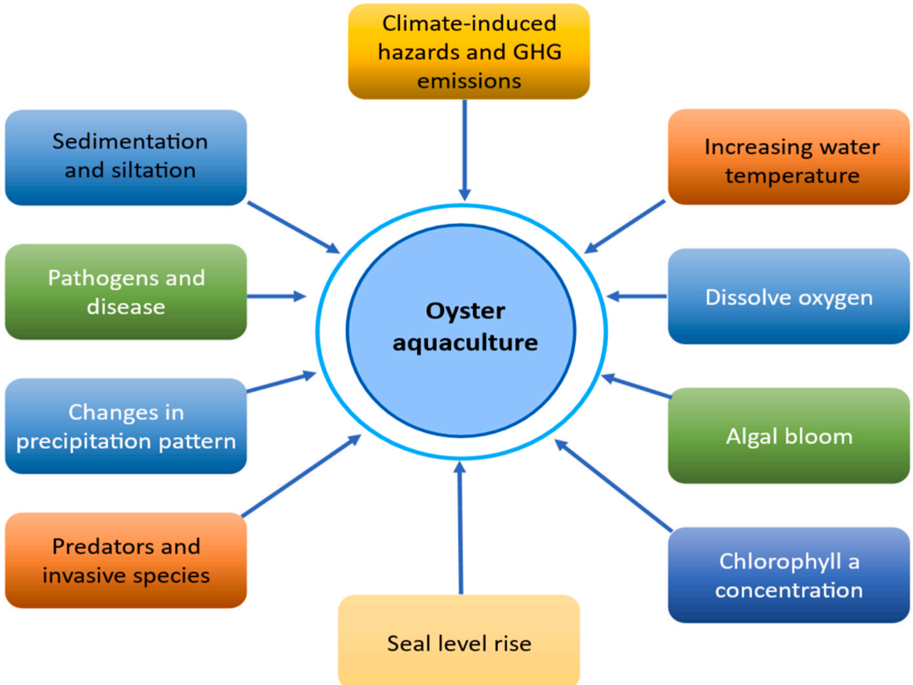


Fig. 7. Some environmental factors affecting oyster aquaculture production.

against increasing the relative danger of predation.

3.14. *Chlorophyll a concentration*

The concentration of chlorophyll *a* in water can be used to characterize the biomass of phytoplankton, preliminarily determine the eutrophication degree of water, and reflect the water quality of lakes (Kim et al., 2021). Therefore, chlorophyll *a* concentration is closely related to environmental factors, which is an indicator of primary productivity in the aquatic ecosystem. In principle, culturing oysters in an area with high chlorophyll *a* concentration is likely to produce quality and marketable size compared with an area with low concentrations. Eutrophic water habitats, particularly those near the ocean such as bays, estuaries, and salt lakes, have high primary productivity output, making them better suited for oyster farming and providing phytoplankton (Umehara et al., 2018). Therefore, oyster farming is frequently carried out in coastal areas due to the rich food availability and convenience. According to Hallegraeff (1993), the consumption of phytoplankton by oysters inhibits excessive phytoplankton growth, including harmful algal blooms (HABs). High primary production is facilitated by the abundant supply of nitrogen and phosphorus input from coastal runoff water emanating from land-based sources. High nutrient loads, however, might cause excessive eutrophication and lead to frequent red tides. Therefore, continuing efforts to reduce organic matter and nutrients such as nitrogen and phosphorus is a serious concern for aquaculture farmers. Furthermore, net zooplankton, and suspension-feeding oysters compete directly for food (Gerritsen et al., 1994). Therefore, in an estuary where primary production is generally high, zooplankton density and biomass per unit volume tend to be ten times higher than in the offshore area (Magalhães et al., 2006; Walkusz et al., 2009).

4. Conclusion and future directions

Fig. 7 illustrates some of the key environmental factors affecting oyster production globally. Oysters are vital natural resources that sustain humans and the aquatic ecosystem. However, climate change and some key factors have impacted its potential for maximum production in many regions. This article discussed the various ways climate change is impacting oyster production. Climate change is causing an increase in acidification and water temperature, adversely affecting its production. To ensure maximum sustainability of oyster aquaculture, climate change, and its induced hazards must be addressed globally and at the regional level. This will ensure food security for countries that are dependent on aquaculture for subsistence and for resource management purposes.

This study recommends that future research should focus on climate-induced hazards such as hurricanes, floods, and storm surges, on oyster aquaculture. Consequently, future research should examine the regional dynamics of climate change to identify locations where oysters or shellfish may be vulnerable to climate change impacts. Additionally, in part 2 of the continuation of this paper, we focused on assessing climate change impacts on oyster production, a framework for modeling oyster production. Lastly, we document mitigation and adaptation measures and knowledge gaps, to be published later.

CRediT authorship contribution statement

Emmanuel Okine Neokye: Writing – review & editing, Writing – original draft, Visualization, Methodology, Conceptualization. **Xiuquan Wang:** Writing – review & editing, Visualization, Validation, Supervision, Funding acquisition, Conceptualization. **Krishna K. Thakur:** Writing – review & editing. **Pedro Quijon:** Writing – review & editing. **Rana Ali Nawaz:** Software. **Sana Basheer:** Visualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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

Data availability

No data was used for the research described in the article.

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