Emerging diseases in Australian oysters and the challenges of climate change and uncertain futures

Running head: Climate change and disease in Australian oysters

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Abstract

Oysters are a valuable and iconic seafood, deeply rooted in Australian culture. However, oysters have always been vulnerable to disease, with disease outbreaks leading to mass mortality events that regularly cost the oyster aquaculture industry millions of dollars and affect livelihoods. Notably, there is evidence that climate change is rapidly causing the emergence of new disease alongside the amplification of impacts of existing diseases. This is because warming, acidification and freshening of coastal and estuarine habitats is affecting the three axes of disease; the host, the external environment and the pathogens. Here we explore how climate change is likely to impact all three axes and disease in Australian oyster aquaculture. Climate change is affecting oyster physiology, leading to weaker immune defences that allow for increased susceptibility to viral and bacterial infections. For example, there is evidence that recent heavy rain events precede oyster disease in estuaries. In addition, climate change is increasing the abundance and virulence of bacterial and viral pathogens, potentially resulting in the introduction of novel disease into new habitats. In order to remain viable, we suggest that the Australian oyster industry needs to enhance selective breeding programs currently underway with a diversification of products and research on emerging diseases to ensure resilience in the sector.

Keywords: Oysters; Disease; Climate change; aquaculture; Vibrio; Bacteria

Background

Oysters are a valuable and iconic seafood, deeply rooted in Australian culture. Historically, oysters were a valued food source for Indigenous Australians and the early colonies following European settlement of Australia (Nell 2001). In recent years, oyster aquaculture has employed thousands of Australians in regional areas, with approximately 1,500 people employed in New South Wales (NSW) alone, where the Sydney rock oyster *Saccostrea glomerata* is the primary product (Barclay *et al*., 2016). Importantly, oyster aquaculture particularly creates employment opportunities for young people in many Australian coastal towns (Pierce and Robinson 2013; Barclay *et al.,* 2016; ABARES 2021). Australia-wide, oyster products are valued at $145 million (ABARES 2012), with the Pacific oyster *Crassostrea gigas* forming the basis of oyster production in Tasmania and South Australia. Beyond the product value, oyster production provides valuable secondary benefits such as employment for regional communities (Pierce and Robinson 2013). For example, Oyster aquaculture products in NSW, mainly *S. glomerata*, are valued at over $50 million annually but with a total value of ~$300 million when the social and economic benefits are factored into calculations (Barclay *et al*., 2016).

Oysters are farmed in estuaries which are among the most urbanised and developed ecosystems in Australia. Over 85% of Australians live within 50 kms of the ocean, and nine of the ten largest cities built on estuaries. Concerningly, climate change, is also impacting these ecosystems, causing estuaries to warm and acidify faster than the oceans (Scanes *et al.* 2020) with a range of consequences for oysters. Oysters and oyster aquaculture are commonly located in estuaries which also provide habitat for commercial fish species, and function to store blue carbon among other ecological services (Fodrie *et al.* 2017).

South eastern Australia (NSW, Victoria and Tasmania) is currently the breadbasket of Australia's oyster production. It is also this region that will experience the greatest effects of climate change as the ocean warming "hotspot" in the Tasman sea warms at a rate faster than the global average (Pörtner *et al.,* 2022). Australia's oyster production is at the global forefront of climate change and provides an opportunity to learn and apply new knowledge regarding disease and climate change to other regions in Australia and around the globe.

Disease has been a major factor causing the decline in oyster aquaculture from the 1970's. NSW oyster production peaked in 1975 at 14 million dozen year^{-1} (Raftos *et al.* 2014), but this number has since decreased to 5.8 million dozen year^{-1} in 2019-2020 (NSW DPI Production Reports 2020). Recent declines have also occurred in Tasmania and South Australia, where between 2008 and 2020 production fell by 750,000 dozen, and 3,350,000 dozen in these states respectively (ABARES 2021). While these declines can be attributed to different causes, a range of diseases have afflicted both *S. glomerata* and *C. gigas* since the

1970s with at least one of these diseases arriving on Australian shores in the last 50 years (Nell 2001). Climate change is predicted to intensify the pressure on oyster farming by warming and acidifying coastal habitats (Scanes *et al.,* 2020), leading to increasing disease events (King *et al.* 2019). Disease occurs as a result of the interactions among host, pathogen and environment, and this disease "triangle" has been used as conceptual model to understand the triggers of disease outbreaks (Scholthof 2007). Here we apply the disease triangle conceptual approach to explore how climate change will impact on the three axes of disease in Australian oyster aquaculture; host, environment and pathogen.

Current and emerging disease in Australian oysters

Crassostrea gigas

The Pacific oyster *Crassostrea* (alternatively named *Magallana*) *gigas* is the most intensely farmed oyster species in the world. *C. gigas* has recently been afflicted by the Pacific Oyster Mortality Syndrome (POMS), which is a disease triggered by the osterid herpes virus OsHV-1, and has devastated the global aquaculture industry, causing up to 35 % mortality on oyster farms in France each year (Fleury et al., 2020). This virus however, is not solely responsible for oyster death, with POMS likely to result from a 'polymicrobial infection'. Research has shown that the OsHV-1 virus supresses the *C. gigas* immune system, allowing bacterial infections, by members of the *Vibrio* genus, to follow. These bacterial infections are then responsible for oyster death, rather than the OsHV-1 virus itself (De Lorgeril *et al.* 2018).

Bacterial infections are common in *C. gigas* and are suspected to be responsible for other diseases. Among these, the disease called "summer mortality" causes significant *C. gigas* mortality in aquaculture during the summer months (King *et al.* 2019). However, until recently the aetiological agent has remained elusive. It is now suspected that summer mortality is caused by a weakening of the immune system caused by heat stress, followed by bacterial infection and oyster death (Siboni *et al.* Submitted, King *et al.* 2019). In-line with this hypothesis, oyster death following marine heatwaves has been shown to be due to bacterial infections, rather than thermal stress to the oyster (Green *et al.* 2019).

In many cases where bacterial infections cause oyster death, the bacteria responsible are suspected to be members of the *Vibrio* genus. *Vibrio* species are commonly implicated in *C. gigas* disease dynamics (Destoumieux-Garzón *et al.* 2020). *Vibrio* pathogens have been identified across *C. gigas* life stages including: *V. alginolyticus*, *V. tubiashii*, *V. anguillarum*, *V. parahaemolyticus* and *V. harveyi* (Go *et al.* 2017; Kirs *et al.* 2011; Lemire *et al.* 2014; Tubiash *et al.* 1970). In a recent study (Siboni *et al.* Submitted) total *Vibrio* abundance as well as the relative abundance of *V. owensii, V. brasiliensis*, *V. jasicida* and *V. harveyi* was significantly elevated when oyster mortality was greatest. *V. owensii* represented the principal driver of *Vibrio* communities and was also the most dominant species in dead oysters. Progressive increases of relative abundance were also observed for *V. harveyi* and *V. campbellii* when oyster mortality occurred. All three *Vibrio* species are known pathogens of marine organisms (Siboni *et al*. Submitted).

In most cases where *Vibrio* have been implicated in the death of oysters, habitat warming has also occurred (Green *et al.* 2019; Petton *et al.* 2013). Analysis of *C. gigas* gene expression patterns have shown a strong interplay among gene expression, the microbiome and temperature (Scanes *et al.* Submitted) and *Vibrio* are known to proliferate in warming conditions (Baker-Austin *et al.* 2013; Vezzulli *et al.* 2015). Vibrio infection may be further aided when oysters experience a weakened immune system at elevated temperatures (Green *et al.* 2019).

Saccostrea glomerata

Disease and climate change will also impact on the Sydney rock oyster, *S. glomerata*. This species is cultured largely on the east coast of Australia, and is responsible for 81% of oyster aquaculture in the state of NSW, where it forms the basis of a culturally iconic industry. *S. glomerata* is also afflicted by diverse diseases, with evidence that their impact may also be exacerbated by climate change (Scanes *et al.* 2021b). The main diseases currently impacting *S. glomerata* are Winter Mortality and QX disease. Winter mortality is a disease mostly recorded within southern estuaries in NSW and strikes during periods of cold weather (Nell 2001). For these reasons winter mortality may become less prevalent as climate change warms NSW estuaries. The impacts of QX disease, however, may be exacerbated. This disease called “Queensland unknown” or *QX* was first reported in the 1970’s and precipitated a significant contraction of the *S. glomerata* industry in New South Wales and Queensland (Nell 2001). QX disease is caused by the haplosporidian protozoan *Marteilia sydneyi*, which invades the oyster’s digestive tract and causes starvation or secondary infection (Nell 1993). QX infection functions by supressing the oyster immune system allowing for infection by opportunistic microbes (Peters and Raftos 2003).

Wet weather events during 2021 and 2022 led to record outbreaks of QX disease amongst the Sydney rock oyster, pushing the oyster industry to the brink of collapse in some regions (NSW DPI 2022). Notably, QX disease is now present in regions that had previously not experienced disease outbreaks including Port Stephens, NSW. Research has shown that periods of low salinity can compromise the immune defence of *S. glomerata* allowing for *M.*

sydneyi infection (Butt and Raftos 2007; Butt *et al.* 2006). There is evidence that this compromised immunity may be triggered during periods of low salinity by the suppression of the *phenoloxidase* system, which can then compromise the immune process (Peters and Raftos 2003).

Selective breeding of *S. glomerata* has significantly improved survivability to QX infection; wild genotype survival rates are often reported as 10% following QX infection, while selected oysters typically can have 70% survival following infection (Dove *et al.* 2013). While this is a significant improvement, selected oysters must be produced in a hatchery setting, thereby limiting the number of oysters available and increasing the price of juvenile oysters. For these reasons the uptake of the selected oysters has been limited in areas where QX has previously not been an issue, leaving farmers vulnerable.

Winter mortality and QX are but two of a range of diseases recorded in *S. glomerata*, with disseminating hemocytic neoplasia, Steinhausia-like infections, Rickettsia-like infections and digenean trematodes having also been observed (Anderson 1996; Green *et al.* 2008). To date these pathogens and parasites have not been responsible for wide-spread commercial losses, but, this may change with altered environmental conditions. Disconcertingly, these diseases were all observed at the northern, warmer extent of the range of *S. glomerata*, which raises the possibility of their southward spread as warming occurs.

Ostrea angasi

The “Native”, or “Flat” oyster, *Ostrea angasi*, is found around southern Australia and was once the basis of a significant wild fishery (Nell 2001). Today it is cultivated in small numbers, mostly in NSW, but attempts to culture the species have occurred in Tasmania, Victoria, and southern Western Australia. *Ostrea angasi* displays fast growth rates and can tolerate warming (Pereira *et al.,* 2020). The greatest impediment to its production has been sporadic outbreaks of the haplosporidian parasite *Bonamia ostreae* that causes the disease Bonamiosis. However, this pathogen is largely found at the northern extent of its range in NSW estuaries (Heasman *et al.* 2004), and few mortalities have been associated with its presence.

Effects of Climate change on the host (oyster)

Research has shown that warming and acidification of estuaries caused by climate change (Scanes *et al.* 2020) can significantly affect both larval and adult Sydney rock and Pacific oysters (Parker *et al.* 2013; Ross *et al.* 2011). Climate change has increased mortality and abnormality of larvae and decreased growth (Cole *et al.* 2016; Kurihara *et al.* 2007; Parker *et al.* 2010). Climate change can lead to decreased shell growth of adult oysters and acidified internal body spaces and altered metabolic rates (Lannig *et al.* 2010; Parker *et al.* 2011; Scanes *et al.* 2017; Wright *et al.* 2014). These impacts on the physical and physiological characteristics may translate into increased disease for oysters.

Disease in oysters is suspected to be the result of change in the environment, which shift the total community of microbes in oysters, known as the microbiome. Microbiomes while vital to the well-being of all organisms, are comprised of both harmful and beneficial bacteria (Wendling *et al.* 2017). Changes to the oyster microbiome alter the oyster immune response (King *et al.* 2019), subsequently triggering opportunistic pathogens to infect oysters (Lokmer and Wegner 2015).

Only recently has research begun to investigate how warming and acidification can interact with the microbiome of oysters. Warming and ocean acidification can alter the bacterial communities of oyster species including the Sydney rock oyster, *S. glomerata*, however, responses of the microbiome are heterogenous among *S. glomerata* genotypes. For example, it has been shown that the impacts of warming and ocean acidification can interact to significantly alter the bacterial community associated with *S. glomerata* when sourced from wild oysters (i.e. not selectively bred for aquaculture) (Scanes *et al.* 2021b). Ocean acidification increased bacterial diversity, but these increases were offset by a loss of diversity under warming (Scanes *et al.* 2021b). Oysters sourced from aquacultural genetic lineages, however, did not experience such significant changes. Rather, the microbiome of only two of the nine tested genetic lineages was significantly affected by either warming or acidification (Scanes *et al.* 2021c).

Genotypic based responses to warming and acidification have previously been found in oysters. For example, ocean acidification had a heterogenous effect on the growth of *S. glomerata* across aquacultural genetic lineages (Parker *et al.* 2011). Similarly, the Standard Metabolic Rate (SMR) of Pacific oysters *C. gigas* was affected by ocean acidification, and the effect was dependant on genetic lineages. Some genetic lineages of *C. gigas* experienced an increase in SMR, and others a decrease (Wright *et al.* 2014). Recent evidence suggests that these genotype-based physiological responses may be driving the response of the microbiome. For example, bacterial communities were shown to strongly correlate with physiological traits, especially SMR (Scanes *et al.* 2021a). When warming and acidification caused a shift in oyster metabolic rates, this triggered a concurrent shift in their microbiome (Scanes *et al.* 2021a). These findings indicate that oyster physiological responses to climate change will likely have flow-on effects to their bacterial communities and subsequently to oyster survival.

Effects of climate change on the environment

Oyster disease is often triggered by changes in their external environment. As estuarine organisms, oysters are faced with frequent environmental changes such as lowered salinity following rainfall. Climate change, however, is increasing the magnitude of these environmental changes. Back-to-back La Nina events in Eastern Australia have delivered record amounts of rainfall with Sydney recording the wettest year-to-date on record and caused much of Australia's east coast to be inundated by floods (BOM 2022).

Oyster farming is an intensive anthropogenic practice that is incorporated within a functioning marine ecosystem. The oysters are therefore interacting and reacting with organisms in their environment. These interactions can have significant consequences for health and disease of oysters. For example, seagrass and macroalgae are often found in the estuarine and coastal ecosystems where oysters are cultured. Seagrasses can act as a microbial filter removing pathogens from the water column, significantly reducing the bacterial load faced by marine organisms (Lamb *et al.* 2017).

Microbial filtering by aquatic vegetation can also reduce disease in oysters. The presence of red (*Solieria*) and brown algae (*Fucus*) significantly increased the survival of *C. gigas* when challenged with the OSHV-1 virus (Dugeny *et al.* 2022). This increased survival was suggested to be facilitated by stabilisation of the microbiome performed by the algae (Dugeny *et al.* 2022). Similar interactions between oyster and aquatic vegetation have also been observed in the Sydney Rock oyster *S. glomerata*. The microbiome of *S. glomerata* was significantly altered by an increased bacterial diversity in the presence of the seagrass *Zostera muelleri* (Garner *et al.* 2021). This relationship was, however, lost when oysters and seagrass were kept together at elevated $p\mathrm{CO}_2$ conditions designed to reflect future (year 2100) atmospheric conditions (Garner *et al.* 2021).

Climate change is predicted to trigger changes in marine ecosystem interactions (Cole *et al.* 2021), including the complete breakdown of ecosystem function in some extreme examples (Harley *et al.* 2017; Harley *et al.* 2006). An alteration or breakdown in current ecosystem interactions could have serious consequences for oyster disease. Already, we know that seagrasses and other aquatic vegetation are important in reducing disease, yet seagrasses are among the most threatened ecosystems on earth, with an annual rate of decline estimated at 7 % year^{-1} (Waycott *et al.* 2009). The future loss of seagrasses and other key species from ecosystems will likely impact oyster health and exacerbate disease.

Effects of climate change on the pathogens

Most of the diseases afflicting *C. gigas* and *S. glomerata* in Australia have emerged in the last century. Some of these arrivals have been more recent than others, with OSHV-1 appearing within the last decade (Jenkins *et al.* 2013). As international shipping and trade into Australia continues to grow, the risk of marine bio-invasions increases. International shipping is the primary means by which goods are transported around the globe, and in-between 2014 and 2018 ships made 34,117 port calls, an increase of 18.8% (BITRE 2020). Shipping is a major vector for marine bio-invasions with ballast water potentially containing a broad range of parasitic taxa, including many protistan and metazoan parasites (Pagenkopp Lohan *et al.* 2022). This ever-increasing ship traffic also poses the threat of oysters hitching a ride amongst fouling communities, and thereby introducing disease into new areas (Minchin and Gollasch 2003).

These risks are also likely to be intensified by climate change. The rapid warming of Australia's east coast is re-drawing the map of thermal niches resulting in range shifts across all levels of ecosystems (Vergés *et al.* 2019). For example, QX disease historically afflicted

QLD oyster growing areas before becoming apparent in northern NSW in the late 1970s, then occurring in the Georges and Hawkesbury rivers near Sydney in 1994 and 2004, respectively. Similarly, in the USA, a parasite *Perkinsus marinus* responsible for the oyster disease called Dermo was limited in its distribution by water temperatures, but, recent warming has permitted its spread throughout the Gulf of Mexico (Burge *et al.* 2014). Conceivably, the recent spread of QX disease may have been facilitated by the extreme warming of NSW estuaries experienced in the summers of 2018 and 2019 (Scanes *et al.* 2020), and may facilitate its range shift further south.

Not all pathogens will benefit from climate change. *Bonamia ostreae* is a protozoan parasite responsible for Bonamiosis in flat oysters of the *Ostrea* genus, including the native flat oyster *Ostrea angasi*. This parasite appears to cause less disease in northern NSW estuaries, and research from Europe has shown that the protozoan has significantly lower survival at 25 °C compared to 15 and 4 °C (Arzul *et al.* 2009). It is, therefore, conceivable that warming oceans will not favour this parasite.

Many oyster diseases are not fatal without the final blow of pathogenic and opportunistic bacteria (De Lorgeril *et al.* 2018; Green *et al.* 2019, Scanes et al., Submitted). Bacteria, including *Vibrio,* like most oceanic organisms are not homogenously distributed over the globe, but rather have distributions governed by temperature and other abiotic and biotic factors (Seymour 2022; Williams *et al.* 2022). Global climate change, such as the strengthening of the East Australian Current is likely to alter these distributions and trigger microbial range shifts (Messer et al. 2020), potentially exposing oysters to new and deadly bacterial pathogens. Climate change is predicted to further intensify heavy rainfall events in eastern Australia as the future climate will bring “more intense heavy rainfall events” (BOM

2020). Short, but intense rainfall events trigger flooding and pulses of freshwater, leading to localised low salinity in estuaries, which can enhance the incidence of diseases such as QX (Raftos *et al.* 2014).

Solutions

Increasing efforts are being made by the aquaculture industry and government to sustain oyster production. Selective breeding remains a popular tool that has significantly reduced the incidence of disease. For example, selective breeding of *S. glomerata* has significantly improved survivability to QX infection (Dove *et al.* 2013). Furthermore, selection of *C. gigas* to overcome OSHV-1 has also shown promising results, with resistant genotypes shown to be capable of maintaining a functional immune system in the face of infection (De Lorgeril *et al.* 2018). Oysters selected for disease resistance have also consistently shown resilience to warming and acidification (Parker *et al.* 2011), with their microbiome remaining stable (Scanes *et al.* 2021c). Transgenerational-plasticity (TGP) has also been shown to reduce the physiological effects of climate change, however, it remains unknown how this may translate to reduce disease (Ross *et al.* 2016). Despite the performance of selectively bred oysters, they are produced in a hatchery, which increases costs to farmers, and in some cases may be prohibitively expensive.

Management actions will be required to curb the spread and potential risk of oyster diseases, particularly in the face of global climate change. Current protocols for the movement of oysters between estuaries will need to be frequently updated to keep pace with disease outbreaks. Diversification will also be key; too often the oyster industry has relied too heavily upon a single oyster species that has then suffered a significant disease event such as occurred in the Hawkesbury River in 2013 (ABC News 2013 “Shell Shocked”).

Flat oysters *Ostrea angasi* and Akoya pearl oysters *Pinctada imbricata* both provide edible alternatives to *S. glomerata* and *C. gigas* and could help the industry to diversify when coupled with consumer awareness campaigns. Culturing oysters alongside seagrass or macroalgae in what is termed “multi-trophic aquaculture” has been shown to buffer some effects of climate change (Falkenberg *et al.* 2021) and may also help reduce the incidence of disease (Garner *et al.* 2021).

Conclusions

Climate change will present unique challenges for the culture of oysters in Australia and across the globe (Figure 1). This review has focused on disease, however, disease is only one of many stressors that will be exacerbated by climate change. Interactions among biological processes and the environment are complex, and must be considered if we are to gain a holistic understanding. Warming and acidification will combine with extreme events, including heavy rainfall and heatwaves to push oysters to their physiological limits, alter the microbiome and divert energy away from immune processes. The impacts of lowered immunity, which will often occur in synergy with the emergence of novel pathogens, will likely result in disease outbreaks and reduced oyster production, with a higher cost placed on the product for the consumer. Emerging diseases such as OSHV-1 and existing diseases like QX may also be exacerbated by secondary, opportunistic bacterial infections. Oyster farmers will likely need to be proactive if they are to successfully manage disease and maintain production under a future climate, however, this will potentially increase the cost of oysters for the consumer.

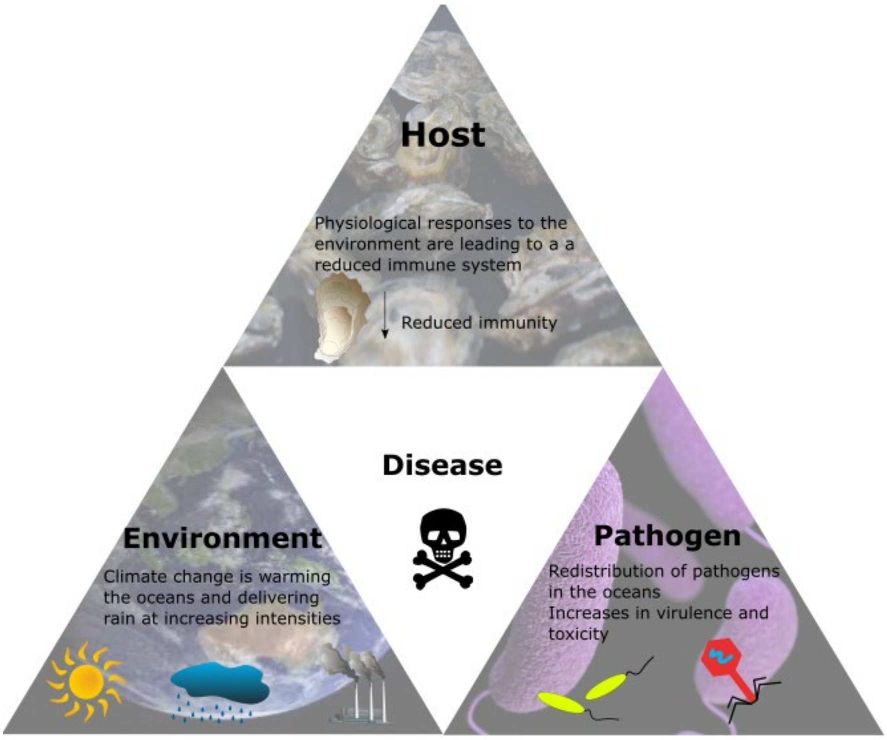

Figure 1. The effects of climate change on oyster production considered within the disease triangle conceptual approach.

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