Continental Shelf Research 273 (2024) 105173

Contents lists available at ScienceDirect

Continental Shelf Research

journal homepage: www.elsevier.com/locate/csr

# Relationships between high temperatures and Pacific Oyster disease and mortality in southeast Tasmania, Australia

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ARTICLE INFO

*Keywords:*
Warm temperature extremes
Marine heatwave
*Magallana gigas*
*Ostreid herpesvirus-1*
Pacific oyster mortality syndrome

ABSTRACT

Warm ocean temperature extremes, including marine heatwaves, have profound impacts on natural marine systems and aquaculture industries across the globe. In Tasmania, Australia, one aquaculture industry that has been significantly impacted by warm temperatures is Pacific Oyster (*Magallana gigas*, previously named *Crassostrea gigas*) farming, due to recurring outbreaks of the virus *Ostreid herpesvirus 1*. Such viral outbreaks are understood to be driven by high seawater temperatures, but the temperature threshold or duration for triggering disease and mortalities remain unclear. This study investigates the relationship between in-situ farm temperatures and oyster disease and mortality on the southeast coast of Tasmania, Australia using daily observations from three oyster growing areas (Pipe Clay Lagoon, Upper Pittwater, and Lower Pittwater) over three seasons. It is found that a 12-day averaged daily mean temperature is an excellent measure of the occurrence of high mortality. Specifically, a 21-day mean of 23.7 °C resulted in a 70% likelihood of high mortality, which is defined here as oyster losses of >15%. On the other hand, for lower levels of disease and mortality, a 12-day average of daily mean temperature gave the strongest relationship. A 12-day mean of 19.7 °C led to 70% probability of some disease and low mortality. The analysis also found in-situ farm temperature generally correlates well with remotely sourced temperature observations, indicating their potential usability for operational management. This study demonstrates a statistical risk analysis framework for the oyster farming industry, helping to improve the understanding of the detrimental impact of high temperatures on Pacific Oysters.

## 1. Introduction

Warm ocean temperature extremes, typically known as marine heatwaves in the case when they are prolonged (e.g. Hobday et al., 2016), have caused widespread concern in recent years (Holbrook et al., 2020; Smith et al., 2021; Oliver et al., 2021; IPCC, 2021). The impacts of warm ocean extremes and marine heatwaves are significant for multiple trophic levels of the marine ecosystem and have socioeconomic implications (Smale et al., 2019; Smith et al., 2022). Numerous mortality and low productivity events resulting from marine heatwaves have been reported by aquaculture and fishery industries for species such as oyster, crab, abalone, and salmon (Pearce et al., 2011; Caputi et al., 2016; Delisle et al., 2020; Meng et al., 2022). Ocean-based fisheries and aquaculture are closely linked to food security and livelihoods and thus increasing temperature extremes will ultimately result in more severe socioeconomic consequences (Wernberg et al., 2013; Pecl et al., 2012; Collins et al., 2019; Meng et al., 2022).

The Tasman Sea is a global warming hotspot with faster warming than the global average rate (Holbrook and Bindoff, 1997; Oliver et al., 2017). In the summer of 2015/16, the Tasman Sea experienced a marine heatwave with the longest duration since the beginning of global satellite records (Oliver et al., 2017). Another marine heatwave around the Tasman Sea extended over a larger area in the summer of 2017/18, which was the most intense event on record for this region (Perkins-Kirkpatrick et al., 2019). The fishery and aquaculture industries in Tasmania, the island state in the southeast of Australia, are vulnerable to high temperatures and have suffered during these marine heatwaves. Examples of such include the mortality of Pacific Oysters, and impaired

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https://doi.org/10.1016/j.csr.2024.105173
Received 21 February 2023; Received in revised form 3 January 2024; Accepted 3 January 2024
Available online 4 January 2024

reproduction of abalone (Pearce et al., 2011; Oliver et al., 2017; Perkins-Kirkpatrick et al., 2019).

The leading cause of Pacific Oyster mass mortality is the microvariant of the *Ostreid herpesvirus 1* (OsHV-1; Segarra et al., 2010). Numerous studies have shown that seasonal virus outbreaks are temperature-dependent, with warm temperature stress being the most crucial environmental factor for mass Pacific Oyster mortality events (Buger et al., 2007; Lionel et al., 2013; Oliver et al., 2017; Pathirana et al., 2022). OsHV-1 infection results in an immunocompromised state for Pacific Oysters, which is followed by recurring disease and large-scale mortalities due to bacterial colonization and infection (de Lorgeril et al., 2018; Delisle et al., 2020; Petton et al., 2021). OsHV-1 is highly contagious (e.g., Ugalde et al., 2018), and typically tends to increase the mortality rate of oysters grown in sheltered and closed environments over other environments (Garcia et al., 2011; Pernet et al., 2012, 2014). Mass oyster infections with OsHV-1 were initially detected in France in the summer of 2008, affecting only Pacific Oysters but triggering a mortality rate over 80% (Segarra et al., 2010). Subsequently, mortalities caused by OsHV-1 have occurred in New Zealand and Australia. In Australia, the disease is often referred to as Pacific Oyster Mortality Syndrome (POMS; Jenkins et al., 2013; Keeling et al., 2014). OsHV-1 was first detected on Pacific Oyster farms in southeast Tasmania in January 2016 (de Kantzow et al., 2017).

In addition to warm temperatures, there are several other factors and environmental variables that can contribute to Pacific Oyster disease and mortality, such as growing rack sizes and heights relative to tidal levels, hydrological conditions, wind, and nutrient concentrations (Dégremont, 2013; Paul-Pont et al., 2013a, 2013b; Whittington et al., 2015; Petton et al., 2021). Environmental factors and intrinsic characteristics of host and virus may have complex interactions along a latitudinal gradient (Fleury et al., 2020). However, Ugalde et al. (2018) found that oyster businesses in Tasmania ranked water temperature as the most important environmental factor influencing mortality, and a majority of those surveyed considered mean temperature of 18–20 °C sufficient for the activation of disease from OsHV-1. Other studies on disease and/or mortality induced by OsHV-1 have found various triggering points at different temperature ranges in different regions (Table 1). Whilst higher temperatures are generally considered the main cause of virus induced disease and mortality (de Kantzow et al., 2016; Whittington et al., 2019; Pathirana et al., 2022), there may be a limit to oyster susceptibility from the virus (Delisle et al., 2018), such that a thermal permissivity window exists.

Prior to the first OsHV-1 outbreak in January 2016, Tasmanian oyster farms produced millions of Pacific Oysters per year, and Tasmanian hatcheries were responsible for approximately 90% of the oyster spat in Australia (Paul-Pont et al., 2014; Mobsby and Koduah 2017; Crawford and Ugalde, 2019). However, the mass mortalities resulting from seasonal reoccurrence of the virus in oyster farming have led to significant economic loss for the entire Australian industry (Evans et al., 2017, 2019). Considerable efforts have been invested into improving farm management practices to reduce OsHV-1 infection mortality and overall impact (Paul-Pont et al., 2014; Pernet et al., 2014; Petton et al., 2015). One of the beneficial programs has been selective breeding, which has operated in Tasmania for several years for biosecurity reasons (Dégremont, 2013; Whittington et al., 2015; Dégremont et al., 2016; Camara et al., 2017). There has also been major progress in preventing the decline of diploid mortalities through selective breeding for OsHV-1 virus resistance (Ugalde et al., 2018).

In this study, we aim to detect whether there is a robust relationship between temperature and mortality in oyster growing regions in Tasmania. The oyster disease and mortality data were supplied by oyster farmers from visual inspection, where some, but not exhaustive, verification was conducted by testing for the OsHV-1 pathogen. The aim is not to explicitly determine the temperatures at which OsHV-1 triggers disease or mortality. Rather it is to find whether there are temperatures at which there is increased likelihoods of Pacific Oyster disease or mortality, recognising that OsHV-1 is a key, but not sole, factor. In addition, we compare temperature data from multiple sources to determine whether remote temperature observations can be reliably utilised in situ.

**Table 1**
A summary of studies linking temperature with disease and/or mortality of Pacific Oysters caused by the virus OsHV-1 or its microvariants in different regions around the world (adapted from Rodgers et al., 2019).

| Temperature range (°C) | Regions | Disease/mortality | Reference |
|---|---|---|---|
| <16 | Marennes-Oleron, France | Infection with low mortality | Renault et al. (2014) |
| 16 | France, Ireland, Spain | Lower threshold value for mortality occurrence | Roque et al. (2012),<br>Clegg et al. (2014),<br>Petton et al. (2015),<br>Renault et al. (2014) |
| ~16 | France, Marennes-Oleron | Mortalities in young oysters | Fleury et al. (2020) |
| 16.2–21.9 | France | Effective virus transmission | Petton et al. (2013) |
| 18–20 | Tasmania, Australia | Disease occurrence | Ugalde et al. (2018) |
| 19–24 | New South Wales, Australia | Disease occurrence | Paul-Pont et al. (2013b), Paul-Pont et al. (2014) |
| 21–22 | New South Wales, Australia | Lower threshold value for mortality occurrence | Jenkins et al. (2013),<br>Paul-Pont et al. (2014) |
| 24 | Mediterranean Thau lagoon, France | Upper threshold value above which mortality stops | Pernet et al. (2012) |
| ~25 | Tomales Bay, California, America | Larval mortality | Cherr and Friedman (1998), Colleen et al. (2006) |
| 26.9–29.0 | France | 50% mortalities in oysters by cohabitation | Petton et al. (2013) |

## 2. Data and methods

### 2.1. In-situ temperature and oyster mortality

This study focuses on data from oyster farming areas in Pipe Clay Lagoon and Pittwater, in the Southeast of Tasmania, Australia (Fig. 1). Oysters farmed in these regions are commercially available, and they are areas in which OsHV-1 was first detected in January 2016 (Ugalde et al., 2018). For the purposes of the analysis, the Pittwater region is divided into two: Upper Pittwater and Lower Pittwater (Fig. 1), and temperature and mortality data was obtained separately for each. Compared with other farming locations in Tasmania, Pipe Clay Lagoon covers a small area but has a high biomass of farmed oysters (Crawford and Ugalde, 2019). As many wild oysters there had a high prevalence of OsHV-1, they may contribute to the reservoir host of the virus. Pittwater is a growing area with extensive intertidal hydrology and poor circulation. Both sites have been shown to be more susceptible to OsHV-1 and have suffered higher mortality rates than other sites in Tasmania (de Kantzow et al., 2017; Crawford and Ugalde, 2019).

Environmental data was collected in each of the three regions using automatic and continuously monitoring data loggers. Near-surface water temperature was measured by submerged sensors provided by The Yield Technology Solutions (Crawford and Ugalde, 2019). The loggers recorded the temperature every 10 min during 1 November to 30 April throughout 2016/17, 2017/18, and 2018/19, with some exceptions. The Upper and Lower Pittwater temperature recordings end on 28 February 2019, but there were also periods of missing and erroneous data in each of the three locations. The in-situ temperature data were first converted to 2-hourly means, partly to smooth any short and large

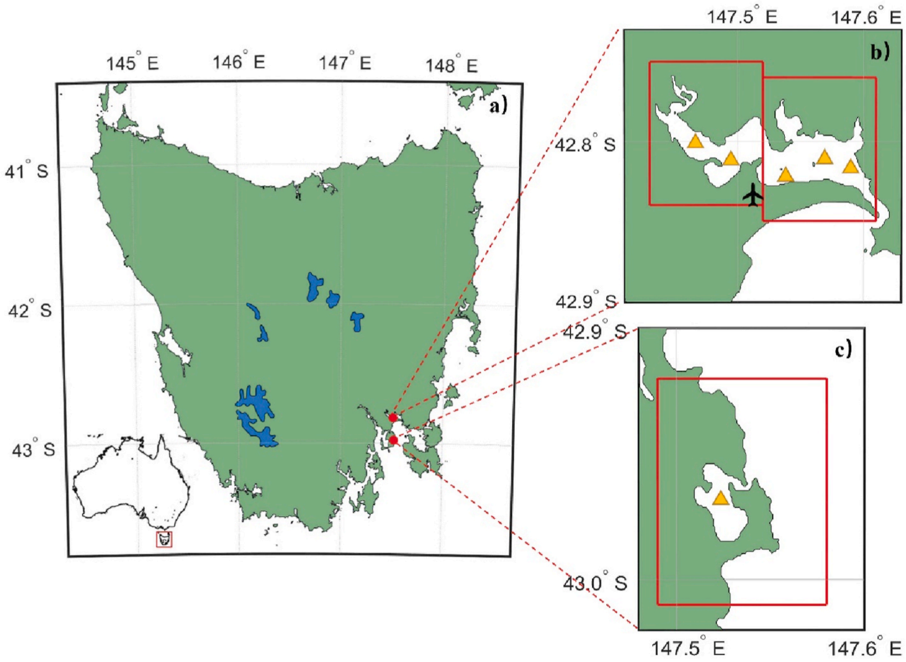

**Fig. 1.** Locations of Pipe Clay Lagoon and Pittwater oyster farming regions. Land is shaded green, inland bodies of water in blue, and open seas in white. (a) The main island of Tasmania. (b) Pittwater. (c) Pipe Clay Lagoon. The red boxes in (b,c) denote 0.1° × 0.1° areas used in sea surface temperature analysis for Upper Pittwater (147.43–147.52°E, 42.75–42.84°S), Lower Pittwater (147.52–147.61°E, 42.76–42.85°S), and Pipe Clay Lagoon (147.49–147.58°E, 42.92–43.01°S). The yellow triangles in (b,c) show the sites where the temperature loggers were situated. The black airplane symbol in (b) indicates the Hobart International Airport (147.50°E, 42.83°S), the location from which air temperature observed from the Bureau of Meteorology is analysed.

temperature variations, but also to resolve short periods of missing data. To fill missing data in periods >2 h, and to correct a 3-month period of erroneous temperature readings in Pipe Clay Lagoon during early 2018, an alternative set of in-situ temperature data was used. The alternative data was from floating sensors measuring temperature every 30 min, but only available during the 2017/18 summer period. There were four floating sensors in Pipe Clay Lagoon and four in Upper Pittwater, and the mean was computed across each, resulting in two sets of temperature readings at 30-min frequency. These were also converted to 2-hourly means, and the missing or erroneous data in the original temperature timeseries' were infilled (where the Upper Pittwater data was also used to correct the Lower Pittwater data). After infilling the missing and erroneous data in the 2 hourly timeseries', daily means, minima, and maxima were computed.

The Pacific Oyster disease and mortality data were collected as part of a project funded by the Australian Government's Cooperative Research Centres Project (CRC-P 2016–553,805; Future Oysters; Crawford and Ugalde, 2019), which included both aquarium experiments with sentinel Pacific oyster spat and farmer observations from real growing sites. The project also involved periodically testing oysters for the OsHV-1 virus with quantitative polymerase chain reaction (qPCR) tests. The tests were conducted under a range of conditions, and at numerous oyster farms around Tasmania (Crawford and Ugalde, 2019). However, for this study, we utilise only one set of the gathered data – those that were from daily visual inspection by experienced oyster farmers. Confidence in the farmers' identification on the OsHV-1-derived mortality has been analysed and discussed by Crawford and Ugalde (2019). A high mortality day was defined as having observed "mortalities > approximately 15% *[of the total cohort]* during summer with water temperatures >18 °C and where there were no other obvious causes of mortality, such as low salinities, extreme air temperatures or excessive biofouling". Hence, one of three levels were recorded for each day: level 0 denoted no indications of disease, level 1 for some sign of disease, such as weakness or failure to close tightly when perturbed, but with low-level mortality (<15%), and level 2 for significant signs of disease with high-level mortality (>15%). The observations were made in Pipe Clay Lagoon and separately for Upper and Lower Pittwater over the period 1 November to 31 May during 2016/17, 2017/18, and 2018/19. There are, however, some limitations and caveats associated with such a visual-observation-based dataset. Firstly, many specific details were not recorded with each observation, such as the counting methods, nor oyster population statistics, such as ages and sizes. Secondly, some of the parameters for the observations were somewhat arbitrarily selected, such as the 15% threshold, or the requirement to exclude "extreme air temperatures" as an alternative "obvious cause of mortality". Despite these limitations, there is nevertheless some value in the dataset, since "on many occasions" (though not recorded when), the "farmer observed disease outbreaks were verified by positive qPCR results for OsHV-1" (Crawford and Ugalde, 2019). Regardless of whether disease or mortality were caused by the OsHV-1 virus, or occurred in any populations, our study aims to determine the relationship between directly observed disease or mortality and temperature within the context of farming industries, and on what timescales.

### 2.2. *In-situ air temperature*

Air temperature observations provided by the Bureau of Meteorology (BoM) from Hobart International Airport were analysed. It is the closest BoM weather station to the two farming regions (Fig. 1). The physical distance between Hobart airport observation station and growing sites in Pittwater and Pipe Clay Lagoon are 3.6 km and 14.5 km. The air temperature data has a half-hourly temporal resolution, and it was downloaded for the period 1 November to 31 May during 2016/17, 2017/18, and 2018/19. Daily mean temperature timeseries were computed.

### 2.3. *Satellite sea surface temperature*

Satellite sea surface temperature (SST) data around Tasmania was analysed from the Group for High Resolution Sea Surface Temperature

(GHRSST) Level 4 Multiscale Ultrahigh Resolution (MUR) Global Foundation SST Analysis, version 4.1, which is available from 1 January 2003 (JPL MUR MEaSUREs Project, 2015). It is a daily dataset, with spatial resolution of 0.01°. The product uses wavelets as basic functions in an optimal interpolation and based upon the NASA Advanced Microwave Scanning Radiometer-EOS (AMSRE). The version 4 MUR Level 4 analysis is representative of foundation temperature, based on the night-time skin and subskin observations (Fiedler et al., 2019).

The daily SST was area-averaged over three $10 \times 10$ grid cell regions (Fig. 1): Upper Pittwater (147.45–147.54°E, 42.75–42.84°S), Lower Pittwater (147.51–147.60°E, 42.78–42.87°S), and Pipe Clay Lagoon (147.49–147.58°E, 42.92–43.01°S). The three timeseries were computed and stored for the period 1 November to 30 April during 2016/17, 2017/18, and 2018/19.

### 2.4. *Statistical modelling*

Our aim is to build a statistical relationship between Pacific Oyster disease and mortality levels and temperature, from which it is possible to estimate oyster mortality risk given an observed temperature sequence or temperature forecast. To this end, the in-situ temperature and oyster disease and mortality data (Section 2.1) is utilised to construct a logistic regression model.

An initial inspection of daily in-situ temperature and disease and mortality levels over a short period (Fig. 2) shows that disease and mortalities were observed over several successive days, rather than single isolated days. Furthermore, the highest impacts did not necessarily occur during the periods of highest temperatures, and conversely, some of the highest temperatures did not trigger impacts (Fig. 2). Hence, the relationship between temperature and oyster mortality does not appear to be straightforward, and thus the effects of temperature accumulation, and delayed or lagged responses, is considered.

Daily temperatures and mortality data were reshaped in two ways to derive the strongest relationships. Firstly, a moving $m$-day mean of the daily temperature was computed, where $m$ was varied between 1 and 25 days (Fig. 3). Secondly, the $m$-day moving mean temperature was compared to the mortality at a lag of $n$-days, where $n$ was varied between 0 and 10 days (Fig. 3). Hence, $m$ represents a period of temperature accumulation, and $n$ represents the delay in mortality response. Together they are denoted the $m$-$n$ relationship (Fig. 3), e.g., the direct comparison of daily temperature ($m = 1$) with same day disease and mortality level ($n = 0$) is denoted the 1-0 relationship. The ranges in $m$ and $n$ values tested follow the suggestions from direct surveys of oyster farmers (Ugalde et al., 2018).

Binary logistic regression is a useful approach to statistically analysing the lagged mortality response to temperature accumulation (King, 2008), where there is a single binary dependent variable, e.g., observed mortality or no mortality. The 3-level disease and mortality data were reduced to two levels in two separate ways. In the first case, level 1 and level 2 instances were merged to form a single level. This may be viewed as testing the temperature effect on no disease (level 0; absence) versus some sign of disease (level 1 or 2; presence). This case is referred to as the test for disease. In the second case, level 0 and level 1 instances were merged, thus testing no or low mortality (level 0 or 1) versus high mortality (level 2). This case is referred as the test for high mortality.

With the disease and mortality data reduced to binary data, a logistic function of the following form was used:

$$p(T) = \frac{1}{1 + e^{-(\beta_0 + \beta_1 T)}} \tag{1}$$

where $T$ is temperature, $p(T)$ is the probability of mortality at the given temperature, and the coefficients $\beta_0$ and $\beta_1$ were fitted numerically using *fitglm* in package *stats* of MATLAB R2022a through maximum likelihood estimation to minimize the sum of the deviation squares between the observed and estimated values of the dependent variable. For all $m$ and $n$, Equation (1) was applied separately to the $m$-day moving mean temperature timeseries versus the $n$-day lagged disease and mortality data, where the disease and mortality data was reduced to two levels in the aforementioned two separate ways. An example of the fitted logistic regression curves for the 1-0 relationship in Pipe Clay Lagoon data is shown in Fig. S1.

The robustness of a particular relationship was estimated by computing the slope at the mid-point (i.e., the 50% probability level). This is assumed to give a reasonable estimate of the strength of the relationship, since as the binary data becomes more clearly separated at the two levels, the slope approaches a step change. It can be mathematically shown that the slope at the mid-point is simply $\beta_1/4$ (Gelman and Hill, 2012).

## 3. Results

### 3.1. *Relationships between temperature and oyster mortality*

The daily mean, minimum, and maximum in-situ temperature of the processed 2-hourly data along with the disease and mortality levels for Pipe Clay Lagoon and Upper and Lower Pittwater are shown in Fig. 4. Both the temporal variability and the magnitude of daily mean temperatures are similar in each of the three regions, particularly in Upper

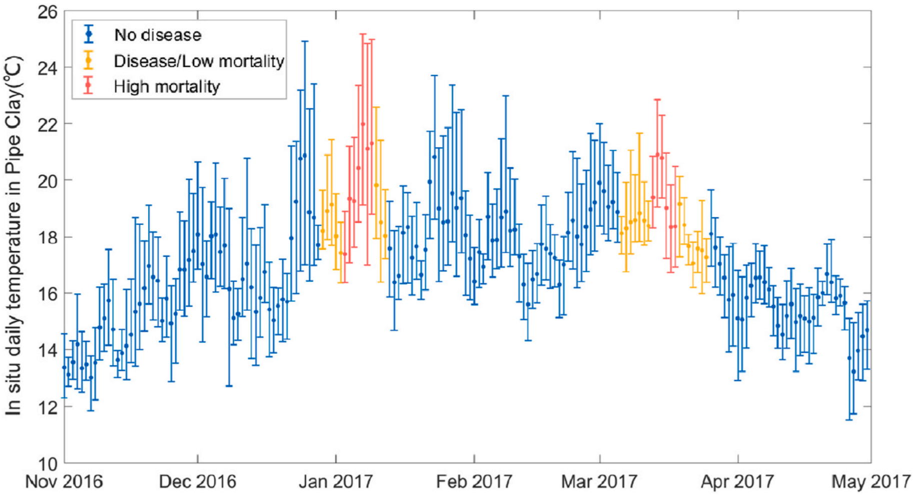

**Fig. 2.** In-situ temperature in Pipe Clay Lagoon during the warm seasons of 2016/17. Points denote the mean values of the daily 10-min temperature and bars denote the range between the minimum and maximum temperature on each day. Different colours denote the three observed disease and mortality levels.

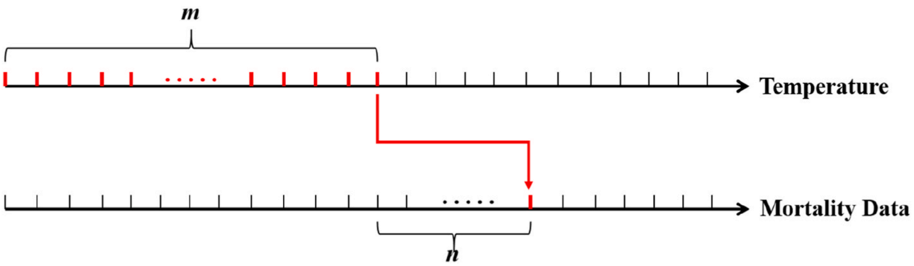

**Fig. 3.** Schematic of the *m*-*n* relationship concept for the daily temperature and mortality data timeseries. The vertical bars denote single days of data. The disease and mortality level on the day indicated in red corresponds to the mortality response due to an *m*-day mean temperature at a lag of *n*-days. All *m*-*n* relationships are tested, with *m* in the range 1–25 days, and *n* in the range 0–10 days.

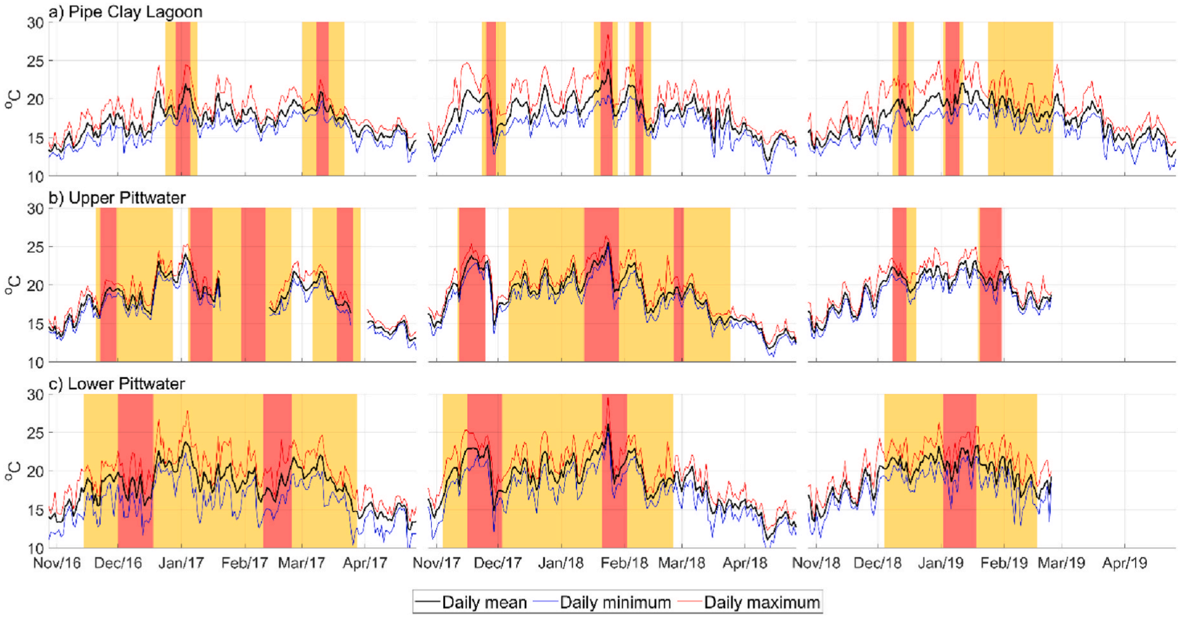

**Fig. 4.** Daily minimum, mean, and maximum in-situ temperatures at the three locations during November to April 2016–2019. Observed disease and mortality levels are indicated with shading, where yellow denotes level 1 (disease/low mortality), and red denotes level 2 (high mortality).

and Lower Pittwater. The diurnal temperature range is generally largest in Pipe Clay Lagoon, and smallest in Upper Pittwater. There are also clear differences in oyster disease and mortality data. There were long periods of disease and mortality in both Upper and Lower Pittwater, persisting almost all of the warm seasons, whereas the disease and mortality periods tended to be shorter in Pipe Clay Lagoon. Note that some periods of missing temperature data remain for early 2017 in Upper Pittwater (Fig. 4b), and those periods were removed from the subsequent analysis.

Histograms of the daily mean temperature and mortality data, in the 1-0 relationship, more clearly show the differences across the three regions (Fig. 5). There are broader temperature distributions in Upper Pittwater (Fig. 5c and d) and Lower Pittwater (Fig. 5e and f) compared to Pipe Clay Lagoon (Fig. 5a and b). There are distinct shifts in the temperature distributions for no disease (level 0) versus some sign of disease and mortality (level 1 and 2), demonstrating at least some link between higher temperatures and oyster mortality. However, differences between the disease/low mortality (level 1) and high mortality (level 2) are less clear, as seen by the similarity in their probability distributions (Fig. 5b–d,f,h), but less so for Pipe Clay Lagoon (Fig. 5b). The combined data for the three locations is also shown (Fig. 5g and h).

### 3.2. *Estimation of mortality risk from multi-day mean temperature*

The robustness of a given *m*-*n* relationship between temperature and mortality was tested by computing the mid-point slopes of the fitted regression curves (Section 2.4; Fig. S1). The procedure was repeated for the full range of *m* and *n* values, in both the tests for disease and high mortality, as well as using daily minimum, mean, and maximum temperature timeseries (Fig. 6). Higher values of mid-point slope indicate stronger relationships between temperature and mortality. Each panel shows a tendency of increasing, then decreasing, values of the slope, for increasing values of *m*. Although there is an exception in the tests for disease (Fig. 6d–f), where for higher values of *n*, there appear to be two maxima for a given *n*. The patterns for the tests for high mortality (Fig. 6a–c) and for disease (Fig. 6d–f) are somewhat different. The largest slope values tend to occur for daily mean temperatures (Fig. 6b–e), as opposed to daily minima (Fig. 6a–d) or maxima (Fig. 6c–f), though there is no obvious difference of the spatial patterns between each set. The largest slope values all occur for $n = 0$, indicating that lag isless important factor.

For the test of high mortality, the most robust relationships were at the 12-0 relationship in the case of daily minimum and mean temperatures (Fig. 6a and b) and at 13-0 with daily maximum temperature (Fig. 6c). In other words, it is found that the strongest relationship between temperature and high mortality is for 12-day moving mean temperature with high mortality data lagged by 0 days. For the tests of disease, stronger relationships were found for longer multi-day means, with the 21-0 relationship returning the largest slope value for daily minimum and mean temperatures (Fig. 6d and e), and the 20-

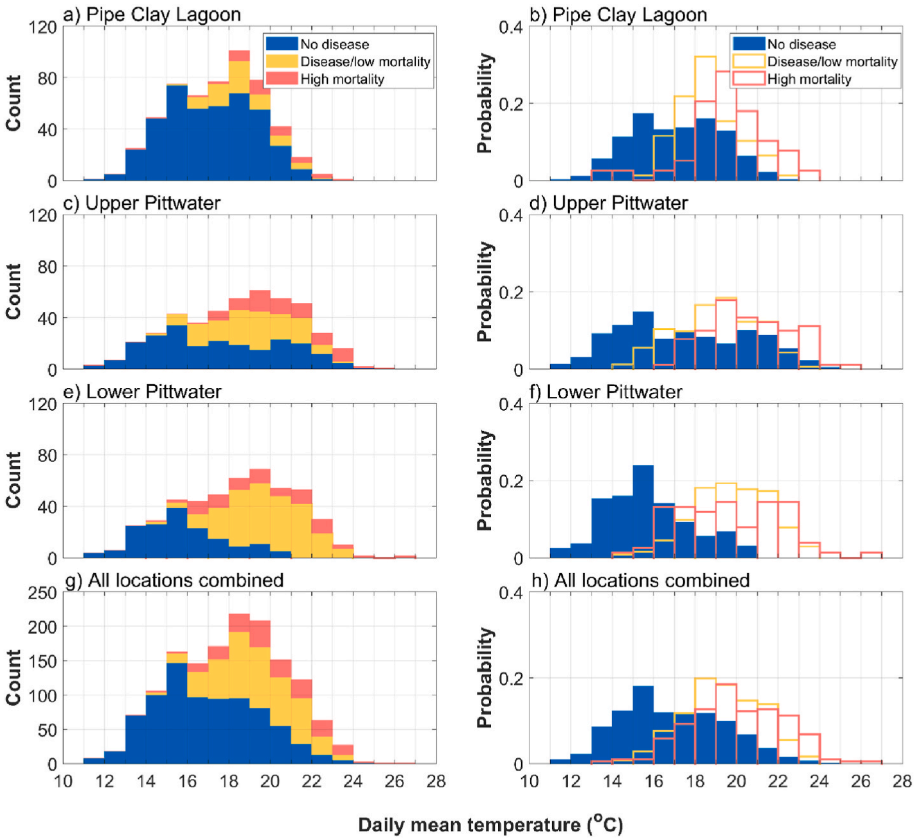

**Fig. 5.** Histograms of counts and probability distributions of three disease and mortality levels in the 1-0 relationship for daily mean temperature. (a,c,e,g) Stacked histograms of the daily mean temperature count. (b,d,f,h) Histograms where the temperatures associated with each mortality level have been normalised by probability (i.e., area under each sums to unity).

0 relationship for daily maxima (Fig. 6f).

Having statistically computed the robustness of each *m*-*n* relationship based on the binary logistic regression, the relationship between temperature and associated risk probabilities can be analysed. The logistic regression fits a probability curve (Fig. S1), from which a risk level (i.e., the probability) can be determined for a given temperature. Conversely, for a given risk level, the associated temperature can be determined. In the limit, where the logistic regression curve approaches a step change, the probability becomes irrelevant, since the temperature will be similar for all probabilities. However, where there is greater uncertainty, it is useful to select a particular probability or risk level. Here the 70% probability level is selected, and the associated *m*-day moving mean temperatures are shown (Fig. 7). These spatial patterns (Fig. 7) generally follow those of the mid-point slopes (Fig. 6), but with opposite sign. This relationship may seem counterintuitive, since cooler temperatures are associated with more robust logistic regression fits, but in fact the larger temperatures in weaker relationship regimes are the result of shallower regression curves (refer to Fig. S1). By definition, lower moving mean temperatures are associated with the minimum temperature analysis (Fig. 7a–d), and higher temperatures using daily maxima (Fig. 7c–f).

To provide another perspective on the data and to demonstrate the relative occurrence rates of moving mean temperatures, histograms of the *m*-day moving mean temperatures giving the most robust relationships with the disease and mortality data are shown in Fig. S2. Note that these temperature histograms are only for the warmer months analysed. In reality there are other cooler temperature periods (outside of November to April), however they are unlikely to be associated with mortality. Furthermore, since a moving mean analysis is adopted, the periods shown in this figure are not necessarily unique, since there is overlap from one *m*-day mean temperature period, and correspondingly in the mortality period. That is, the mortality periods are discrete, but prolonged (Fig. 4). Nevertheless, generally for warmer temperatures, there are increasing proportions of oyster mortality (Fig. S2). Lastly, although the multi-day mean temperature that results in a 70% risk level has rarely been observed for the high mortality case (Figs. S2a–c), it is well within the observed distribution for disease or low mortality (Figs. S2d–f).

A summary of mean temperatures associated with a range of probability levels, along with their associated uncertainties is given in Table 2. Three probabilities (50%, 70%, and 90%) are shown to infer three risk temperature zones (moderate, strong, and severe risk). The temperatures associated with given probabilities for high mortality are higher than that for the probabilities of disease, as expected. For example, a 21-day mean of minimum temperatures of 18.5 °C is associated with a 70% probability of disease (Table 2b), whilst a 12-day mean of minimum temperature of a similar temperature (21.3 °C) is associated with a 50% probability of high mortality, and a higher temperature (22.9 °C) is needed for a 70% probability (Table 2a). Additionally, as the risk probability increases, the uncertainty range for the risk temperature expands, especially for high mortality (Table 2a). The greater uncertainty at higher probabilities is due to sparser data, i.e., fewer occurrences of temperatures at the warm tail of the observed distribution.

### 3.3. Utility of remote temperature sources

The in-situ temperatures are compared with BoM air temperature (from Hobart International Airport) and satellite SST measurements, to test whether such remote sources might provide utility for oyster farmers. A strong correlation with BoM air temperature, for example, would improve the reliance on temperature forecasts for managing

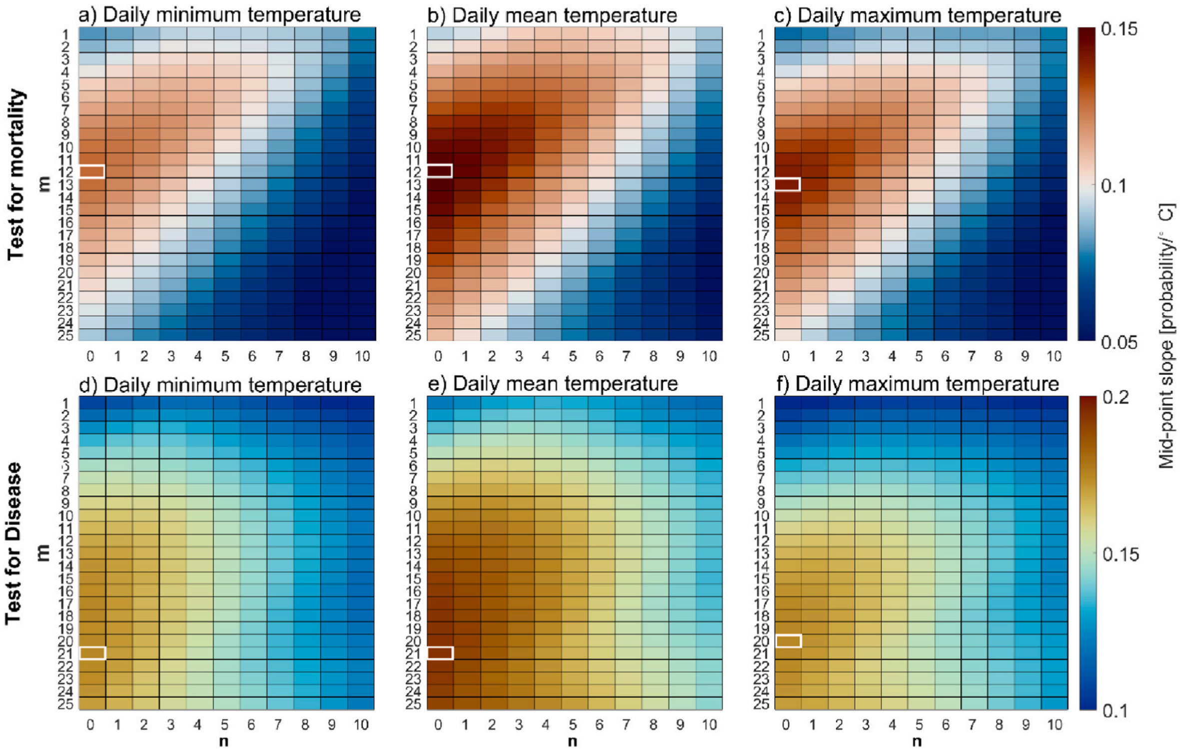

**Fig. 6.** The mid-point slope of the logistic regression curves for each *m*-*n* relationship using combined temperature and mortality observations from Pipe Clay Lagoon, Upper Pittwater, and Lower Pittwater. Higher values indicate stronger relationships, and the units are probability/°C (refer to Section 2.4 and Fig. S1). The y-axis is for the *m*-day moving mean of temperature, and the x-axis for the *n*-day lag. (a–c) Tests for high mortality, using the daily minimum, daily mean, and daily maximum timeseries respectively. (d–f) Tests for disease, using the daily minimum, daily mean, and daily maximum timeseries respectively. The maximum slope in each panel is indicated by a white box. Note that the colorbars span different ranges in the upper and lower panels. Figures for each separate location are included in the supplementary material (Figs. S3, S4, S5).

potential risks. As to whether the forecasts themselves are accurate or not is another matter, but forecasted extreme temperatures will aid preparedness. Satellite SST observations, on the other hand, provide another opportunity for monitoring local, but also nearby remote temperatures. The timeseries of daily mean in-situ temperature, daily mean BoM air temperature, and daily satellite SST are shown during November 2017 to April 2018 for each of the three regions (Fig. 8).

There is reasonable correspondence between in-situ water temperature and BoM air temperature (Fig. 8), even for the more remote Pipe Clay Lagoon (Fig. 1), though the air temperature exhibits more variability. This is potentially due to complex atmospheric dynamics or the fact that air has much lower specific heat capacity than water. Therefore, air temperature varies more greatly, even though there is the same amount of heat energy added or removed in the air as in water. The in-situ temperature also has complex variations, potentially due to other environmental factors (Ugalde et al., 2018), since the in-situ temperature sensors were in fixed positions, and readily influenced by hydrologic and other weather factors. The satellite SST is also in agreement with the other two sources, but it exhibits much less variability. Whilst satellite SST is useful for estimating longer term mean temperatures, the satellite SST does not capture the day-to-day variability.

The correlations between in-situ temperature and the other two sources were calculated for the duration of available data during 2016–2019 (Table 3). The daily mean in-situ temperature correlates strongly with daily mean BoM air temperature at all three locations. But the correlation is generally weaker with satellite SST, as expected from Fig. 8, apart from at Pipe Clay Lagoon. The satellite SST observations are corrected to represent night-time temperature (Section 2.3), which would tend to represent detecting the cooler portion of daily temperatures. Therefore, correlations were also calculated with daily minimum in-situ temperature, but they do not yield stronger values (Table 3).

## 4. Discussion

This study provides new insight into the application of temperature analysis to help assist farm management decisions. Specifically, the analysis used data from Pipe Clay Lagoon, and Upper and Lower Pittwater to assess the relationship between temperature and Pacific Oyster disease and mortality levels. The analysis confirmed the strong link between oyster mortality and high temperatures as seen in previous studies (Petton et al., 2013; Pernet et al., 2014), and extended the research by Crawford and Ugalde (2019) to examine multi-day mean temperature effects. There is scope for further extension of this work to projected hazard identification, by incorporating the identified thresholds with a proposed marine heatwave hazard index (Kajtar and Holbrook, 2021). Similar analysis can also be adapted to other aquaculture or fishery for which warm temperature extremes are a concern, such as salmon or abalone industries.

Pacific Oyster mortality due to the OsHV-1 virus is multi-faceted, with elevated temperature being a clear, but not sole, driver. Other environmental factors, such as tidal currents, wind, nutrient concentrations, and phytoplankton, may all play some additional part in triggering mass mortalities following extreme temperatures (Berthelin et al., 2000; Peeler et al., 2012; Pernet et al., 2012; Ugalde et al., 2018; Petton et al., 2021). For oyster farms near estuaries, hydrodynamics plays a critical role in the transmission of the virus through water connectivity (Pernet et al., 2012; Paul-Pont et al., 2013a). Latitudinal gradient of oyster farming aeras could also alter the risk of Pacific oyster mortality induced by the virus by interacting with the health status of the pathogen and oysters (Fleury et al., 2020). Therefore, temperature cannot be considered the only factor driving the mortality of Pacific Oysters. There are a range of other factors that may contribute to Pacific Oyster mortality from the OsHV-1 virus. Some of these additional factors

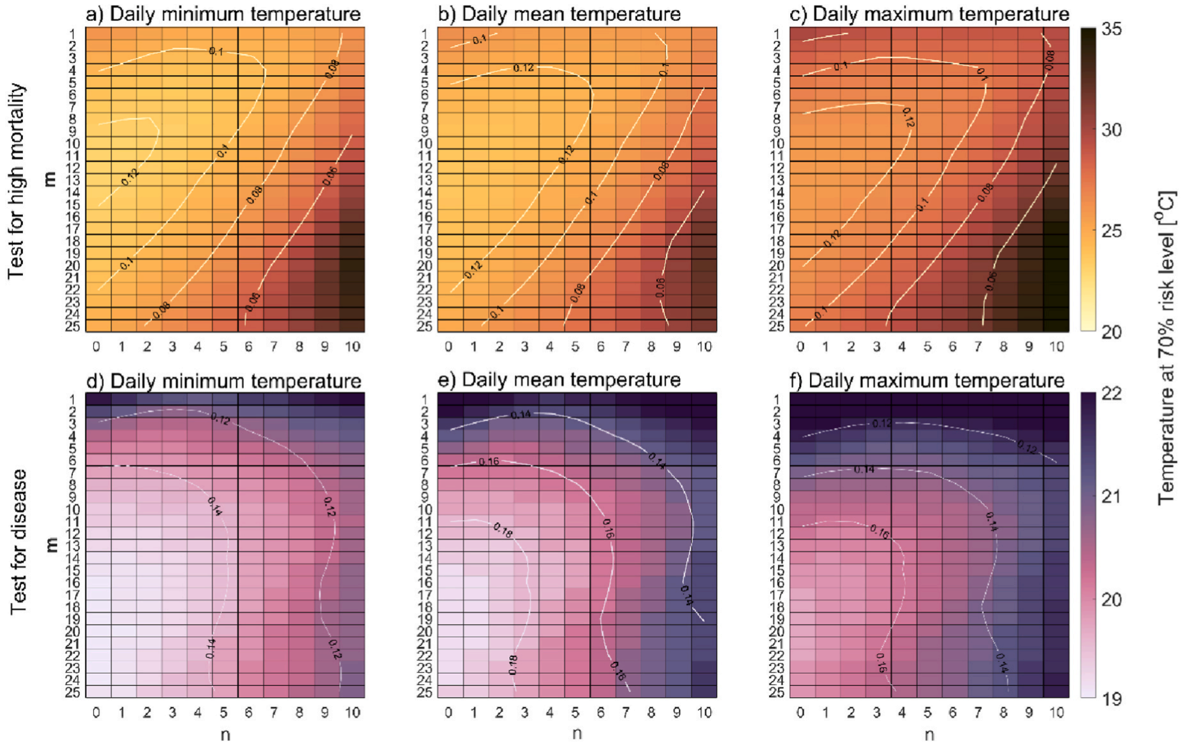

**Fig. 7.** Moving mean temperature corresponding to 70% risk probability on the logistic regression curve for all *m*-*n* relationships using combined temperature and mortality observations from Pipe Clay Lagoon, Upper Pittwater, and Lower Pittwater. The y-axis is for the *m*-day moving mean of temperature, and the x-axis for the *n*-day lag. (a–c) Tests for high mortality, using the daily minimum, daily mean, and daily maximum timeseries respectively. (d–f) Tests for disease, using the daily minimum, daily mean, and daily maximum timeseries respectively. Contours denote the mid-point slope values at 0.02 probability/°C intervals (Fig. 6). Figures for each separate location are included in the supplementary material (Figs. S6, S7, S8).

**Table 2**
Mean temperatures (°C) associated with thresholds of probability for (a) high mortality, and (b) disease, using combined temperature and mortality observations from Pipe Clay Lagoon, Upper Pittwater, and Lower Pittwater. The most robust *m*-*n* relationships are shown. Uncertainties are calculated through the 95% confidence interval of the logistic regression.

(a).

| Probability of high mortality | 12-day averaged daily min | | 12-day averaged daily mean | | 13-day averaged daily max | |
|---|---|---|---|---|---|---|
| | Temperature | Uncertainty | Temperature | Uncertainty | Temperature | Uncertainty |
| 50% | 21.3 | 20.0–22.6 | 22.3 | 21.2–23.3 | 24.1 | 23.0–25.3 |
| 70% | 22.9 | 21.1–24.8 | 23.7 | 22.2–25.2 | 25.7 | 24.1–27.3 |
| 90% | 25.7 | 22.9–28.5 | 26.0 | 23.7–28.2 | 28.1 | 25.6–30.5 |

(b).

| Probability of disease | 21-day averaged daily min | | 21-day averaged daily mean | | 20-day averaged daily max | |
|---|---|---|---|---|---|---|
| | Temperature | Uncertainty | Temperature | Uncertainty | Temperature | Uncertainty |
| 50% | 17.2 | 16.8–17.6 | 18.6 | 18.3–19.0 | 20.3 | 19.9–20.7 |
| 70% | 18.5 | 18.0–19.0 | 19.7 | 19.3–20.1 | 21.5 | 21.1–21.9 |
| 90% | 20.6 | 19.6–21.6 | 21.5 | 20.7–22.2 | 23.5 | 22.6–24.3 |

may relate to oyster physiology, such as their spawning rates, ages, and sizes (Dégremont, 2013; Health and Welfare, 2015). Studies have suggested that older and larger oysters are able to develop stronger resistance to OsHV-1 (Dégremont et al., 2015, 2016; Hick et al., 2018). In addition to the intrinsic factors of oysters, the threshold of OsHV-1 from the virus perspective for disease or mortality expression was also linked with temperatures (de Kantzow et al., 2016). Disease and mortality could only be triggered for a particular lethal dose of virus. We also acknowledge that there is a thermal permissivity window at which the OsHV-1 virus triggers disease, e.g., at 29 °C, the susceptibility of oysters to the virus has been found to decrease (Delisle et al., 2018). However, the upper limit of the window is well beyond the range of the observed maximum temperature in our study region of southeast Tasmania.

There is some advantage in studying mortality in real-world conditions, as opposed to solely under laboratory conditions. But clearly there are many factors that cannot be controlled. An example is the timing and duration of extreme temperature periods. When a period of mortality occurs due to warm temperatures, weaker oysters are more susceptible and die-off more readily, leaving behind stronger specimens. Thus, when the next warm period occurs, even if it is more intense, there may be fewer mortalities because those that remain are better adapted. Clearly linking mortalities with the OsHV-1 virus, rather than other or compound factors, is also crucial.

There is value in observing temperatures from remote sources and forecasts because they are operational and can provide an early warning of elevated temperatures. In this study, air temperature observations, as

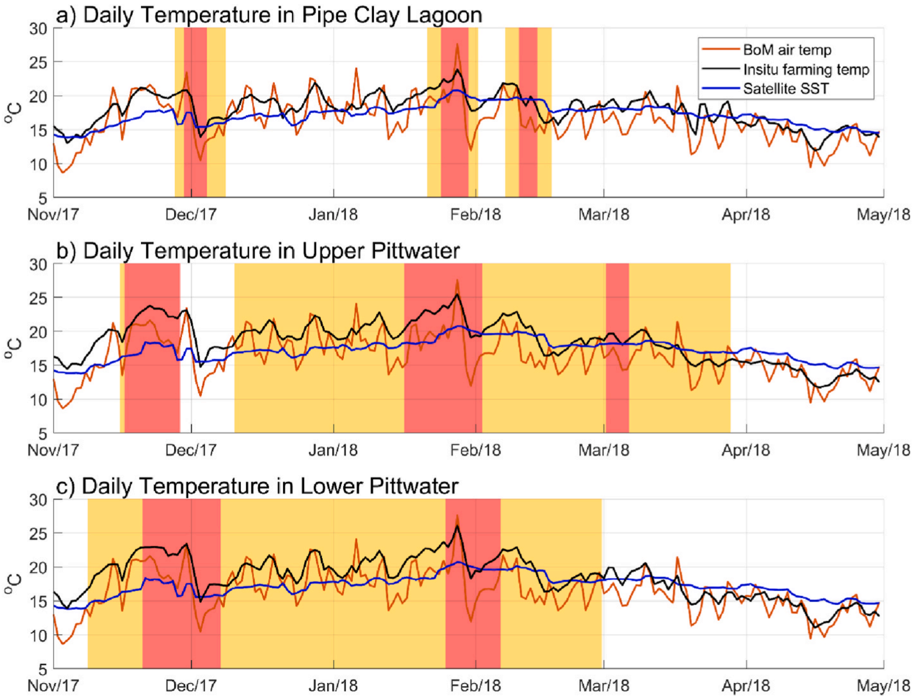

**Fig. 8.** Daily temperature from three sources during November 2017 to April 2018 in the three regions. (a) Pipe Clay Lagoon, (b) Upper Pittwater and (c) Lower Pittwater. The daily mean BoM air temperature from Hobart Airport is the same in each panel, and it is compared to daily mean in-situ temperature, and the local area-averaged satellite sea surface temperature. Yellow shading denotes periods of disease/low mortality, and red shading denotes high mortality.

**Table 3**
Pearson's correlations between in-situ daily mean temperature and satellite sea surface temperature and BoM daily mean air temperature in Pipe Clay Lagoon, Upper Pittwater, and Lower Pittwater. The values in parentheses are the correlations with in-situ daily minimum temperatures.

| | Satellite SST | BoM |
|---|---|---|
| Pipe Clay Lagoon | 0.77 (0.76) | 0.75 (0.73) |
| Upper Pittwater | 0.64 (0.60) | 0.73 (0.72) |
| Lower Pittwater | 0.63 (0.55) | 0.78 (0.72) |

well as satellite SST observations were considered. Skilful forecast of temperature is informative for fisheries and aquaculture management and conservation (Salinger et al., 2016; Dunstan et al., 2018; Holbrook et al., 2020). Specifically, forecasts of a few days to weeks provide opportunities for active strategies to be implemented (White et al., 2017), such as early harvesting or relocation of aquaculture species. Although satellite data only provide day by day observations, rather than forecasts, they may provide some opportunities for early warning. For example, mesoscale warm eddies have the potential to significantly influence coastal water temperature and even drive marine heatwaves (Li et al., 2023). Observations of such eddies as they move along the coast toward the region of interest might in future be utilised to inform forecasts of elevated temperatures. However, it is necessarily to understand the limitations of remote temperature measurements since they record different information. Remote air temperatures are not necessary the same as local water temperatures, and satellite observations can be hindered by atmospheric conditions, such as cloud cover amount and distributions. Future studies might focus more on exploring how remote temperature sources could complement in-situ data. For instance, testing the accuracy of remote satellite observations for estimating local farm water temperature may contribute to the monitoring and management of the oyster disease and mortality occurrences.

Although the present study focused on the risk of oyster disease and mortality from POMS in specific regions of Southeast Tasmania, Australia, it is hoped that the findings may inform risk management there but also elsewhere in the world. Oyster growers may now have a clearer indication of what multi-day mean temperatures are most impactful, and hence could monitor past observations and future forecasts, and plan accordingly. For instance, modifying harvest strategy and handling oysters ahead of the heating period (Peeler et al., 2012; Ugalde et al., 2018). Periodically chilling treatment would reduce oysters' exposure accumulation as well. Pacific Oysters in other regions are likely to respond in different ways, for a variety of reasons, but the logistic regression approach used here could similarly be applied to temperature or mortality datasets elsewhere. While we found that multi-day temperature accumulation had a stronger effect than multi-day lag on oyster disease and mortality, the lag effect may have been somewhat underestimated as the multi-day averaging incorporates some lag effect due to averaging over the past days. Furthermore, even though only the multi-day average temperatures with the most robust disease and mortality responses are highlighted, the results that have been generated could in principle be used to guide the risk estimate for any multi-day mean temperature and lag. For example, given an average temperature reading for the prior *m* days, the risk level for the upcoming *n*th day can be returned, along with its associated confidence level. Such a tool could be developed and made available as an easy-to-use smartphone application, for example. However, it is recognised that the approach used here may also be further refined, for example by including more environmental variables. The timespan of the data used here was also somewhat limited. Nevertheless, an approach in relating oyster disease and mortality to temperature has been demonstrated, and with greater data availability, confidence levels on risks can be substantially improved.

## 5. Conclusions

This study investigated the relationship between temperature and the disease and mortality levels of Pacific Oysters due to OsHV-1 in three farming regions in Southeast Tasmania. It was found that mortality is more strongly related to multi-day temperature accumulation, rather than daily temperature. That means continuous warming plays a more significant role than single-day extreme events. More specifically, disease and high mortality levels were related with temperatures at different thresholds and multi-day durations. A 21-day average of daily mean temperature over 19.7 °C has a 70% probability of triggering disease in Pacific Oysters, while a 70% probability of high mortality occurs with a 12-day average of daily mean temperature over 23.7 °C. Notably, this does not mean that disease or mortality will not occur with temperature extremes spanning less than these number of days, but these are the intensities and durations at which the relationship was found to be most robust.

Comparison of in-situ temperature with remote sources found that both the daily mean and minimum temperatures in Pipe Clay Lagoon are well correlated with high-resolution satellite SST. In contrast, the temperatures in Upper and Lower Pittwater are more strongly correlated with air temperature observed by the Bureau of Meteorology at Hobart International Airport. With further improvements on accuracy and longer-range outlooks, forecasts from such remote temperature sources might be more reliably utilised to undertake short-term active interventions protecting Pacific Oysters from OsHV-1.

## Data availability

The raw and processed temperature and Pacific Oyster disease and mortality data are available from: https://github.com/jiaxins1028/Temperature-oyster_mortality. Air temperature at Hobart Airport, Tasmania, Australia is provided by the Australian Bureau of Meteorology, and is available via http://www.bom.gov.au/climate/dwo/IDCJDW7022.latest.shtml. Group for High Resolution Sea Surface Temperature (GHRSST) Level 4 Multiscale Ultrahigh Resolution (MUR) Global Foundation SST Analysis is available at https://podaac.jpl.nasa.gov/dataset/MUR-JPL-L4-GLOB-v4.1.

## CRediT authorship contribution statement

**Jiaxin Shi:** Data curation, Formal analysis, Writing – original draft, Writing – review & editing. **Jules B. Kajtar:** Methodology, Supervision, Writing – review & editing. **Hakase Hayashida:** Methodology, Supervision, Writing – review & editing. **Sarah C. Ugalde:** Investigation, Supervision.

## Declaration of competing interest

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.

## Acknowledgements

This work was conducted with support from the Institute for Marine and Antarctic Studies, University of Tasmania and Ocean University of China. JS and JBK acknowledge ongoing support from the Australian Research Council Centre of Excellence for Climate Extremes (CE170100023). The authors acknowledge the previous work by Christine Crawford and Zijie Zhao that was supported by the Department of Industry, Innovation and Science (Grant number: FN30643) and funded by Future Oysters CRC-P (PI Christine Crawford), and thank the Bureau of Meteorology, supported by the Australian Government, and NASA's Jet Propulsion Laboratory for making their data available. The authors are very grateful to members of the Tasmanian oyster industry for participating in surveys and providing their observations that led to the generation of the dataset used in this study. Thank you to Neil J. Holbrook and Peter G. Strutton for their feedback on an early version of this manuscript.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.csr.2024.105173.

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