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Coupling habitat-specific temperature scenarios with tolerance landscape to predict the impacts of climate change on farmed bivalves

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ABSTRACT

Due to climate change, heatwaves are likely to become more frequent, prolonged and characterized by higher peak values, compared with climatological averages. However, the thermal tolerance of organisms depends on the actual exposure, which can be modulated by environmental context and microhabitat characteristics. This study investigated the frequency of occurrence of mass mortality events in the next decades for two species of farmed bivalves, the mussel *Mytilus galloprovincialis* and the clam *Ruditapes philippinarum*, in a shallow coastal lagoon, characterised by marked diurnal oscillations of water temperature. The effect of heatwaves was estimated by means of tolerance landscape models, which predict the occurrence of 50% mortality based on the exposure intensity and duration. Scenarios of water temperature up to the year 2100 were modelled by combining two mechanistic components, namely: 1) monthly mean water temperatures, simulated using a hydrodynamic model including the heat budget; 2) daily oscillations, estimated from the harmonic analysis of a twenty year-long site-specific time series of water temperature. Scenarios of mean daily sediment temperature were estimated by means of a cross-correlation model, using as input the water temperature one: the model parameters were estimated based on a comprehensive set of site-specific water and sediment temperature observations. The results indicate that for both species the risk of mass mortality rapidly increases starting from the 2060s. Furthermore, the daily patterns of water temperature seemed to be relevant, as overnight it falls below the predicted mortality thresholds for a few hours. These findings suggest that further studies should address: 1) the improvement of tolerance landscape models, in order to take into account the integrated effect of repeated non-lethal stress events on mortality rate; 2) the prediction of environmental temperature in specific habitat, by means of both process-based and data driven models.

1. Introduction

With ongoing climate change, extreme climatic events, such as heatwaves, are predicted to increase in frequency, intensity, and duration. The thermal tolerance of organisms depends on the last two heatwave characteristics: according to Rezende et al. (2014) tolerance landscape models can predict mortality, usually of 50% of a population, based on temperature level and exposure time. The tolerance curves of bivalves, in particular, are characterised by a wide range of thermal sensitivity parameters (see Rezende et al., 2014).

In 2019 molluscs farming contributed to 19% of all mariculture in the Mediterranean region (Carvalho and Guillen, 2021). Italy is one of the top producers, contributing to 12% in weight and 10% in value, and in terms of molluscs producing large quantities of Mediterranean mussels (*Mytilus galloprovincialis*; 62000 tonnes) and Manilla clams (also known as Japanese carpet shells, *Ruditapes philippinarum*; 31000 tonnes) (Carvalho and Guillen, 2021), which account for around 95% of total national shellfish production and contributing 77% to the EU clam production (EUMOFA, 2022). Bivalve farming has been recently advocated as a 'restorative aquaculture' practice with some climate mitigation potential, due to a lower greenhouse gas emission compared to other protein sources and to the potential for the development of climate-friendly culture methods (Jones et al., 2022). At the same time, the activity is in itself at risk from climatic changes (Froehlich et al., 2018; Stewart-Sinclair et al., 2020), which can lead to mass mortalities due to heat waves, seen already in 1999 and 2003 in the north-west Mediterranean sea (Coma et al., 2009; Garrabou et al., 2009). Heatwaves can cause mass mortality of many shellfish species, including

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oysters, mussels and clams: (Raymond et al., 2022): relevant economic implications were already observed in summer 2021 in the Pacific Northwest (Smith et al., 2021; WSG news, 2021). Marine heatwaves are increasing in frequency, intensity and duration worldwide (Oliver et al., 2018) including the Mediterranean sea (Pastor and Khodayar, 2023). In the northern Adriatic lagoons, reductions in terms of production have already been recorded in the last decade (2012–2021). Therefore, understanding how these species are coping with thermal stress and developing models that could be used to predict mass mortalities is very relevant also for the shellfish farming sector.

Bivalves inhabit different dimensions of the marine environment, both in the 'horizontal' dimension, occurring from coastal to offshore waters, and in the 'vertical' dimension, being part of both the epi- and endo-benthos. In terms of the 'horizontal dimension', the coastal zones have been historically preferred as farming locations (Primavera, 2006), being logistically more convenient (ease of access, possibility to anchor structures, less risk from adverse weather events) and transitional coastal areas, such as lagoons (Aliaume et al., 2007), can be especially advantageous, providing more protection and frequent farm access. Shallow coastal ecosystems are, in fact, important shellfish culture areas (Bartoli et al., 2016), and they provide about 90% of the Italian production of the clam *Ruditapes philippinarum* (Trevisan, 2011), which comprises about 85% of the EU production (FEAMP, 2014). Mussels also tend to be farmed in shallower areas, although offshore locations are being considered (Mascorda Cabre et al., 2021).

Looking at the 'vertical dimension', cultivation can take place all the way in the water column down to the seabed and into the sediment, depending on the species' ecological niche. Transitional coastal bodies can be more susceptible to climate change induced warming and acidifications (Scanes et al., 2020), however they are also subjected to marked fluctuations in temperature, often associated with those of oxygen and salinity (Kaplan et al., 2003; Newton and Mudge, 2003). Tides can also lead to strong fluctuations in sediment temperatures, in particular in very shallow or intertidal areas, due to the exposure to direct solar radiation and direct contact with the atmosphere, (De Wilde and Berghuis, 1979). The short-term dynamic of water and sediment temperature could have important implications on the tolerance to heat waves, as stress may be followed by periods of recovery, facilitating acclimation (Oliver and Palumbi, 2011): organisms response, therefore, depends on both the mean external temperature and its variability (Bozinovic et al., 2011).

Microhabitats can also modulate climate stress (Scheffers et al., 2014; Suggitt et al., 2011), with different habitat typologies presenting different heat conductivities (e.g. white vs. black substrates on a rocky shore (Lathlean and Minchinton, 2012); presence of layers of benthic species in intertidal habitats (Wethey et al., 2011); north - south facing rocks (Firth et al., 2015)), leading to the mitigation of harsh conditions. In coastal environments, microhabitats may be represented by different substrate types, for example different sediment features, i.e. colours and particle size, modulate heat exchanges with the water column. Sediment may take longer than water to warm up at the beginning of the summer season and then retain heat for longer in the later part, an effect that will depend upon sediment porosity (Zhang et al., 2022). Furthermore, sediment types and porosity are also characterized by marked and short scale spatial variability in transitional coastal areas (e.g. Molinaroli et al., 2014, 2009), thus making it hard to predict the evolution of sediment temperature based on that of the water column in shallow water transitional water bodies.

The aim of this work was to estimate the effect of heat waves on bivalve mass mortality in the next decades, up to the year 2100. This goal was achieved by applying a tolerance landscape model to two species, namely the Mediterranean blue mussels *Mytilus galloprovincialis* (Lamark, 1819) and the Manila clam *Ruditapes philippinarum* (Adams & Reeve 1850) - which co-occur in the same geographical zones but inhabit two distinct vertical layers: water-column (farmed mussels) and upper sediment layers (farmed clams). The two species are predicted to have different responses to temperatures, with *R. philippinarum* often considered a highly tolerant species (e.g. Domínguez et al., 2021). Tolerance landscape models allow the estimation of mass mortalities in relation to the exposure time of marine organisms to a given temperature level, whereas simple approaches, (e.g. as in Galli et al., 2017) consider only a threshold level, above which mass mortality is expected to occur. The exposure time to a given temperature was estimated using both water column and sediment temperatures scenarios (Castro-Olivares et al., 2022), as described in the next section.

2. Methods

2.1. Case study description

The approach described in this section was applied to the Lagoon of Venice in the framework of a comprehensive study, aimed at assessing the effects of temporary closures of the lagoon inlets. A model chain was applied to the prediction of mussel and clam mass mortalities due to heat waves in the next decades: to this aim, one-year long water and sediment temperature scenarios were estimated for the beginning of each decade, from 2020 to 2100. As, at present, shellfish are farmed in the southern part of the Lagoon of Venice, the study was focused on the two clam and mussel farms shown in Fig. 1.

Monthly water temperature at sites B1 and B2 for the years 2020–2100 were obtained using as The model SHYFEM-CLIM, i.e. the 2D updated version (Melaku-Canu et al., in prep.) of the finite elements model SHYFEM – Shallow water Hydrodynamic Finite Element model, previously validated for the Venice Lagoon (Umgiesser et al., 2004) was applied over the whole lagoon. The model predicts the Lagoon water temperature based on wind stress, heat fluxes, evaporation rate and sea

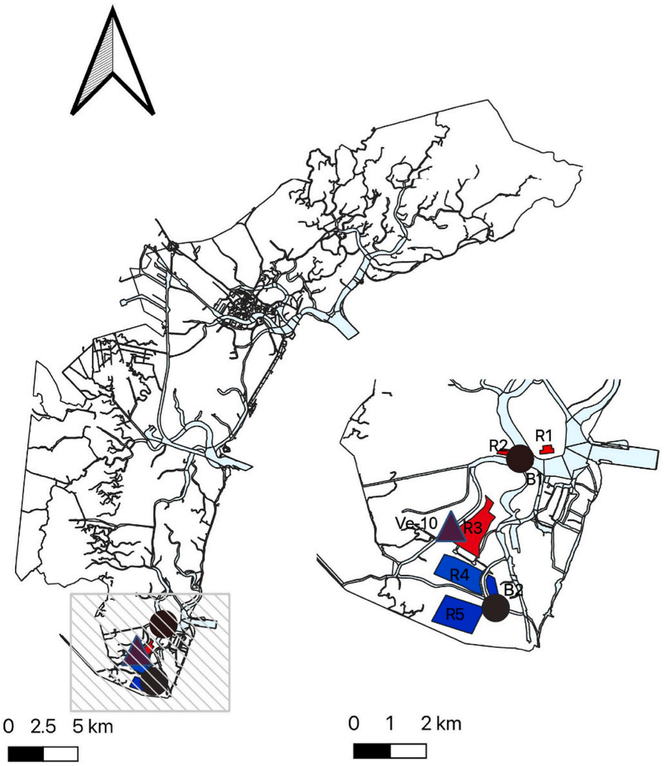

Fig. 1. Map of the Venice Lagoon showing the main canals (light blue), with a zoom on the southern part which shows the shellfish farming areas and the temperature sampling site. Water temperature: B1 (black circle – top) and B2 (black circle – bottom); sediment temperature: R1, R2, R3 (red), R4, R5 (blue). Reanalysis of water temperature data 2008–2018: Ve-10 station (black triangle). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

surface temperature. Data for meteorological forcings were obtained from the CCLM model (COSMO_CLM) for the RCP 8.5 2006–2100 scenario(s) (Bucchignani et al., 2016; Zollo et al., 2016). This is the worst-case scenario, in which GHGs emissions are assumed to increase throughout the 21st century, leading to a pCO_2 concentration of about 1200 ppm by the end of the 21st century (Fox-Kemper et al., 2021). Boundary conditions at the sea inlets (water temperature and salinity) were taken from CMCC-NEMO(Reale et al., 2022; Solidoro et al., 2022). Marine water levels at the inlets were estimated from (Zanchettin et al., 2021), applying a linear trend up to the projected value of 0.71 m at the end of the century (for the 8.5 RCP scenario, using the 50° percentile of the ensemble model projections). Details on the formulation of SHYFEM are given in (Oddo et al., 2005). The model simulates heat transport and water temperature at each node of the high-resolution domain, which is made up of an unstructured mesh of 6017 nodes and 10407 elements.

The daily fluctuation component of Eq. (1) was estimated from the re-analysis of water temperature time series collected at site Ve10 from 2008 to 2018. The data were routinely collected by the 'SAMANET' network, consisting of ten multi-parametric sensors deployed across the whole lagoon that collected half-hourly data. Data for this study were made available for the years 2008–2018.

The sediment temperature model (2) was calibrated using a time series of water temperatures collected at site B1 and B2 in the years 2020–2021 and a time series of sediment surface temperatures measured using low-cost sensors (Thermochron iButton DS1921G.F5) placed at a depth of about 3.5 cm at sites R1-R5 during the same time period (deployment 01/07/2020-26/05/2022).

2.2. Water temperature scenarios

Marine heat waves are classically defined as seawater temperatures exceeding a seasonally varying threshold for at least 5 consecutive days above the 90th percentile of daily temperature (Hobday et al., 2016). In this case we extend the definition to consider species-specific thresholds (Bertolini and Pastres 2021): since these may differ between species at short time scales, the time series to be used for estimating the exposure time should be characterized by, at least, a daily frequency. However, in shallow water bodies, the daily oscillation of water temperature in summertime can be relevant: a statistical analysis applied to the case study here presented showed, for example, that the daily range in a typical July day is about 8% of the daily mean. These assumptions were validated in preliminary tests showing the relevance of hourly fluctuations on the outcome of the tolerance model compared to just using the daily trend. Therefore, in this study we used hourly time series of water temperatures for the decades 2030–2100 as input, which were modelled as detailed below. The hourly modelling frequency was maintained for the sediment temperatures as well, to allow for better comparability of the results for the respective species.

An additive structure of the water temperature time series was assumed: (e.g. Laanaya et al., 2017)

$$T_w(t) = T_r(t) + S(t) + \varepsilon(t) \tag{1}$$

in which $T_w(t)$ represents water temperature at a given site, $T_r(t)$ the trend which, in this case, includes also the annual seasonal component, $S(t)$ the seasonal component representing a daily oscillation and $\varepsilon(t)$ the stochastic term, normally distributed.

The first component was estimated by interpolating the site-specific mean monthly values predicted by the SHYFEM-CLIM model which is described above (ref. chapter 2.1).

The daily oscillations, $S(t)$, were estimated based on the reanalysis of a 10 year-long site-specific hourly time series of water temperature, collected by the SAMANET network (ref. chapter 2.1). The data was pre-processed, in order to remove outliers and anomalous data. Isolated missing values were linearly interpolated. Afterwards, the data set was split into 12 subsets, one for each month, as the amplitude of daily temperature oscillations depends on the time of the year. The time series pertaining to each month were analysed to extract the most important periodic components. To this aim, the trend was removed using splines and the Fast Fourier Transformation was applied to the residuals. The daily oscillations for each month were then obtained by averaging the phase and amplitude estimated for the most important frequencies.

2.3. Sediment temperature scenarios

In order to apply the tolerance landscape model to *Ruditapes philippinarum*, which could be representative of endo-benthic species, a scenario of surface sediment temperature was constructed. In shallow water bodies, heat exchanges at the water-sediment interface are the main drivers of the surface sediment temperature dynamics, which could be simulated using process-based models (Pivato et al., 2020). As an alternative, the sediment temperature could be related to that of water, using a site specific statistical model (Pivato et al., 2020). In this study, we selected the second approach and tested the following linear model:

$$T_{sed}(t) = a + b\,T_w(t) \tag{2}$$

in which $T_{sed}(t)$ and $T_w(t)$ are the time series of average daily sediment and water temperature. The two parameters were estimated from a comprehensive set of surface sediment temperature, collected at sampling sites (R1-R5) close to two multiparameter buoys for the monitoring of water quality parameters, including water temperature (located at B1 and B2).

Sediment temperature time series collected at sites R1- R2- R3 and R4-R5 were aggregated, as a preliminary analysis showed that within each group temperature differences were very small, considering also the low resolution of the measures (0.5 °C). The sediment at three sites (R1-R2-R3) were coarser, compared with the those in R4-R5), which were characterized by higher mud percentages, (unpublished data): this is consistent with their location in a more confined area of the lagoon.

A qualitative comparison among the sediment and water time series showed that the water temperature is higher than the sediment one in spring-summer and lower in autumn-winter: therefore, the sediment temperature model (2) was calibrated by splitting the data set into a spring-summer set – from March 21st to September 23rd; and an autumn-winter set – from September 24th to March 20th. In order to smooth the discontinuity in sediment temperature predictions at the beginning of spring and autumn, due to the different parameterization, the sediment temperature s was simulated as a weighted average of the summer and winter model outputs two weeks before and two weeks after the beginning of the respective sets. The weights were taken as proportional to the difference between a given day and the end/beginning of the model application time window. As this this study is focused on heat waves, only the spring-summer sediment temperatures were used as input for the tolerance landscape model. Nevertheless, the above-described smoothing was maintained, as it was deemed to provide a more realistic scenario for the whole year.

2.4. Tolerance model

The tolerance model, Eq. (3), based on the theory described in Rezende et al. (2014), predicts the occurrence of a 50% mortality event (LT50) based on the exposure time, t_e [minutes], at a given temperature T_{k0} [°C]. CT_{max} is the LT_{50} within 1 min of exposure, and z is a constant that characterizes the sensitivity to temperature change.

$$T_{ko} = CT_{max} - z\,log_{10}(t_e) \tag{3}$$

The model (3) was applied to two species commonly farmed in Mediterranean lagoons and coastal areas: the Mediterranean blue mussel *Mytilus galloprovincialis* and the Manila clam *Ruditapes philippinarum:* the former is farmed in the water column while the latter on the seabed. A tolerance model for *R. philippinarum* was already developed by

Bertolini and Pastres (2021) and the same procedure was followed to estimate the model parameters for *M. galloprovincialis,* based on literature data, searched using 'Web of Science', 'Scopus' and 'Google scholar', for adult individuals (Anestis et al., 2007; Feidantsis et al., 2020; Mesas and Tarifeño, 2015). The study presented lethal temperatures and the time (in days or hours, then transformed in minutes) in which 50% mortality occurred. These data were then all collated for parameter estimation, using an ordinary least square minimization (using the *lm* function in R), with the logarithm of the exposure time as the explanatory, independent, variable and the lethal temperature as the dependent variable.

Equation (3) was used in this study to predict the occurrence of 50% mortality events as a consequence of heatwaves, using the above-mentioned water and sediment temperature time series as input. The methodology, presented in detail in Bertolini and Pastres (2021) involves two steps: 1) a temperature range is defined, in this case starting from the minimum temperature used in the literature assay and the maximum recorded temperature, and scanned using 0.1 °C temperature step; 2) for each value, the exposure time, is estimated from the temperature time series by counting the consecutive hours spent at or above it. The longest exposure time for each temperature was then compared with the one that, according to eq. (3), would cause a 50% mortality.

3. Results

3.1. Water and sediment temperature scenarios

The procedure for the estimation of the water temperature scenarios was applied to the site B1 in Fig. 1. The results of the reanalysis of the 12 detrended monthly data sets obtained from the 10-year long time series collected at site Ve-10 indicated, that the most important periodic component was associated with the daily frequency, thus suggesting that in this shallow water area the main forcing of the daily oscillation of the water temperature is the solar irradiation. The phase and amplitude were estimated for each year and then averaged (Table 1), thus obtaining the seasonal component as:

$$S_m(t) = A_m\ (\cos(2\pi\ (t / 24) + \varphi) \tag{4}$$

in which t is time [hours] and the subscript "m" refers to the month of the year. This component was added to the daily means. The resulting water temperature scenarios for the eight decades are presented in Fig. 2.

A linear model was applied to find the relation between the aggregated sediment surface temperatures (R1, R2, R3 or R4, R5) and the respective water temperature time series (taken at B1 and B2 respectively). The parameter estimates can be seen in Table 2 below.

Water scenarios with daily fluctuation predicted a maximum temperature of 34.35 °C compared to the maximum temperature estimated with the trend only (31.34 °C). In the sediment, maximum temperatures of 30.9 °C were forecasted at S1 and 30.2 °C at S2.

Table 1
Means and standard deviations of the phases and the amplitudes for each month of the year. In bold values from the summer set that this study focused on.

Month	Phase (radians)	Amplitude
January	−0.344 ± 1.69	0.1677 ± 0.065
February	1.3938 ± 0.035	0.469 ± 0.103
March	**1.7424** ± **0.038**	**0.8788** ± **0.248**
April	**1.8304** ± **0.154**	**0.9142** ± **0.216**
May	**1.7443** ± **0.143**	**0.7917** ± **0.142**
June	**1.6479** ± **0.12**	**0.9561** ± **0.119**
July	**1.5391** ± **0.098**	**1.2316** ± **0.053**
August	**1.5657** ± **0.13**	**1.1892** ± **0.169**
September	**1.6367** ± **0.055**	**0.814** ± **0.087**
October	1.8037 ± 0.153	0.4315 ± 0.09
November	1.2228 ± 2.132	0.1372 ± 0.042
December	−0.467 ± 2.116	0.22 ± 0.096

Fig. 3 shows in the upper panel three temperature scenarios: the red line indicates the monthly mean values computed using the Shyfem model and the black one the daily fluctuation. The lower panel shows the differences in the estimations of risk, based on the monthly values and water temperature scenarios including the daily fluctuations, for the temperature of 26 °C, the lowest temperature used in the literature tolerance assays. As one can see, all monthly means in 2020 were below the threshold, but the fluctuations occasionally exceed 26 °C. In 2050 the trend exceeds the threshold in summertime, but the fluctuations bring the temperature below it, and, therefore, the duration, black line, is low. In 2100, the number of consecutive hours of exposure to temperatures higher than 26 is similar in the two case.

3.2. Tolerance landscape scenarios

The results of the estimation of the parameters of the tolerance landscape model for *Mytilus galloprovincialis* are presented in Table 3. A comparison between the two species shows that both CT_{max} and *z* of *Mytilus* are lower than the *R. philippinarum* ones, resulting in shorter period of tolerance at the upper end of the tested temperature range, but a longer tolerance period at the lower end of the stressful temperatures (Fig. 4). For example, according to the model, at a temperature of 26 °C clam mass mortalities are expected to occur after 49 days but only after 109 days for mussels. Mortalities are becoming more similar at a temperature of 27.5 °C with clam mass mortalities expected after 27 days and mussels after 29 days. This inverts at higher temperatures, for example at 30 °C clam mass mortalities are expected to occur after 12 days and mussel after 3 days, further dropping at a temperature of 32 °C when clam mass mortalities are expected to occur after 6 days, but in less than 1 day for mussels (Fig. 4).

The results of the application of the tolerance landscape models to the water and sediment temperature scenarios are shown in Fig. 5a and b respectively. Results show that for both species heat waves which could be lethal, in terms of LT50, may frequently occur, in the last decades of the century (2060 onward), with the time threshold being surpassed more often and for longer periods at the lower end of the tested temperature range. For example, *Mytilus galloprovincialis* will be at risk of surpassing their tolerance for temperatures of >26 °C for up to 60 days from 2066 onwards, their tolerance of temperatures >30 °C for1-2 days in the latter part of the century (2090) and even surpass their tolerance for temperatures of 34 °C, even if only for part of the day (4 h), starting already from 2080. *Ruditapes philippinarum* will be subject to similar risks with its tolerance at temperatures of 27° surpassed for a shorter time (up to 22 days in 2066) but reaching lower peak temperatures (29.4 °C which could be surpassed for up to 15 days) (Fig. 5a–b). With regards to the sediment temperatures, some differences can be observed between the two sites, with cultivation at site S1 (coarser sediments) being riskier in earlier decades (2060–2080) and surpassing the threshold at higher temperatures in later decades (2080 onwards) compared to S2 (finer sediments, Fig. 5b).

The water temperature scenario which included the daily fluctuation led to different results when estimating mortality risks. The fluctuations of temperature above the trend, even if for limited periods, could be enough to pass the mortality threshold: this is especially true at the higher end of the temperature range, with short lethal exposure time. Fluctuations below the trend, on the other hand, allow for recovery time, this is particularly important at the lower end of the temperature scenario, where trends would predict a surpassing of the time-temperature threshold (Fig. 6).

4. Discussion

With this study we combined tolerance landscape with environment site-specific scenarios. The tolerance landscape for the two species revealed some differences: *Mytilus galloprovincialis*, an epibenthic

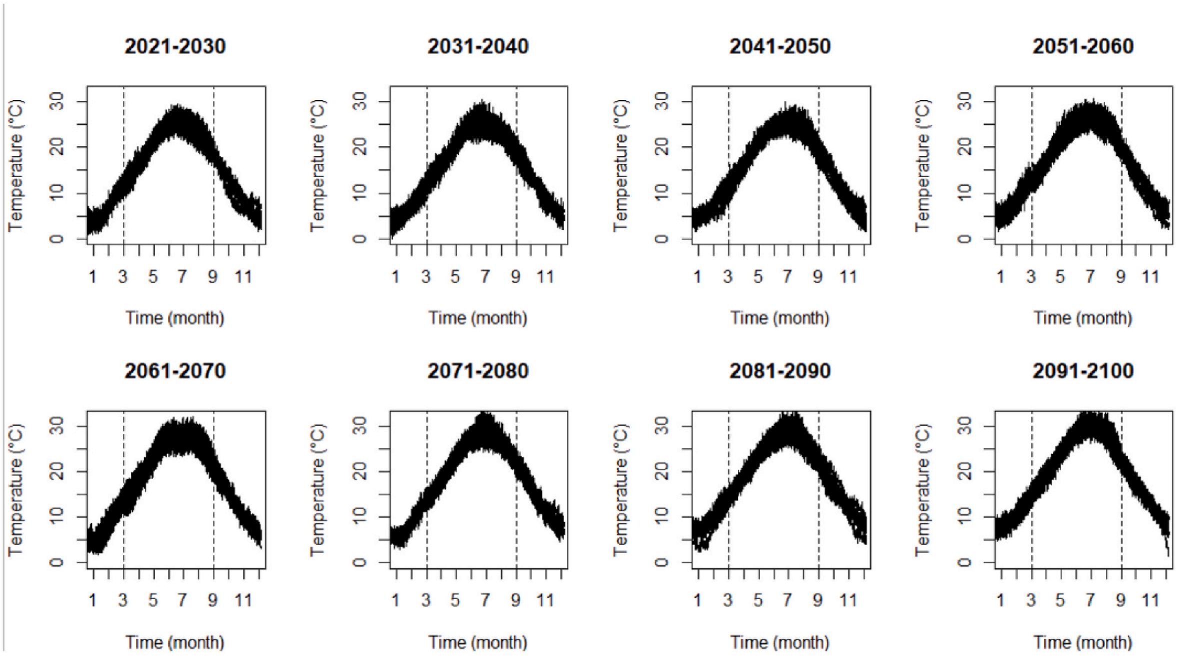

Fig. 2. Water temperature scenarios of daily water temperatures for each of the 8 decades considered. Vertical lines represent the regarded summer interval (March–September included).

Table 2
Parameters of the linear model for the estimation of sediment surface temperature and their standard errors for the summer data set.

	intercept (a) [°C]	slope (b) [-]	
R1-3	0.39 ± 0.49	0.96 ± 0.02	Adj $R^2 = 0.96$; $p < 0.001$
R4-5	0.45 ± 0.52	0.94 ± 0.02	Adj $R^2 = 0.95$; $p < 0.001$

Table 3
The results of the estimation of the parameters of the tolerance landscape model (CT_{max} and z) for the two bivalve species.

Parameter	*Ruditapes philippinarum*	*Mytilus galloprovincialis*
CT_{max} [°C]	54.7 ± 2.3 (Bertolini and Pastres 2021)	39.7 ± 1.7 (this study)
z [°C]	5.7 ± 0.7 (Bertolini and Pastres, 2021)	2.6 ± 0.4 (this study)

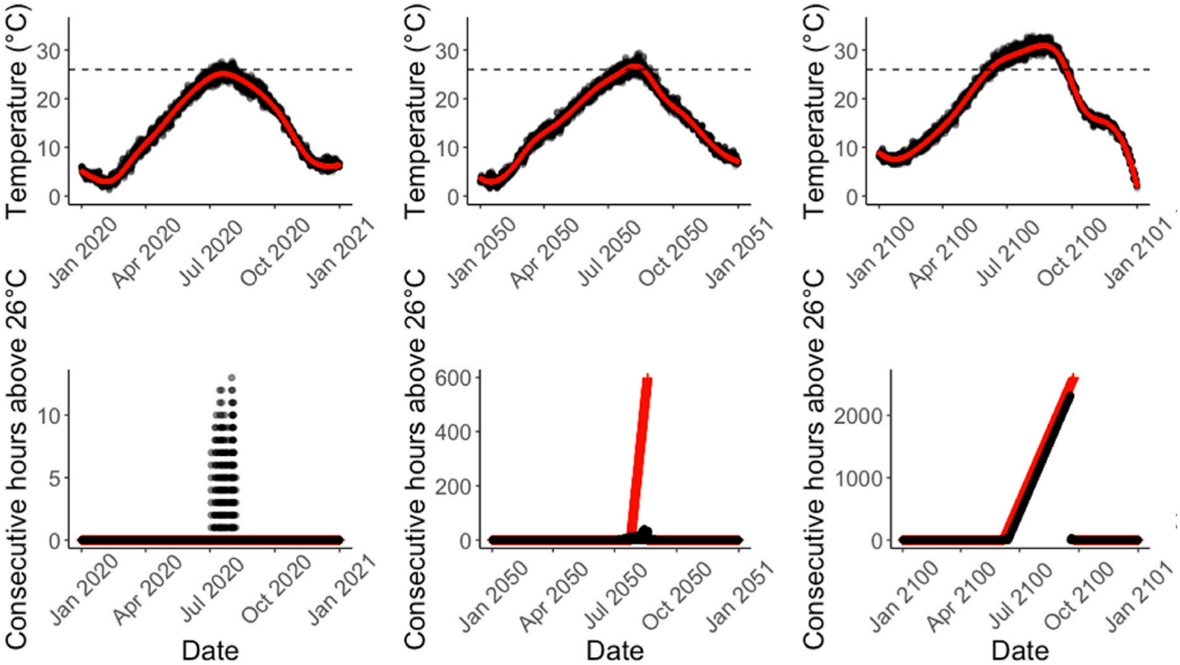

Fig. 3. Top row: examples of water temperature scenarios (2020, 2050, 2100), red line indicating trend based on monthly means, black dots represent the full fluctuation scenario. Horizontal line at the threshold of 26 °C. Bottom row: examples of calculations of consecutive hours above 26 °C for the trend (red) and fluctuation (black) scenario. Note the different scale on the y axis for the three years. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

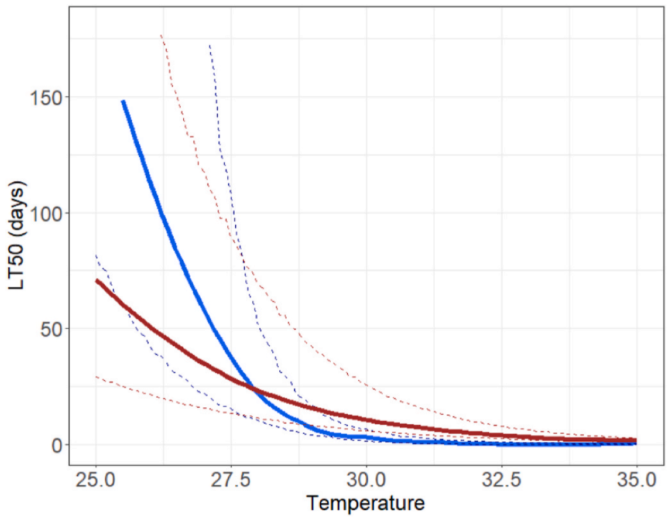

Fig. 4. Tolerance landscape curves of *Mytilus galloprovincialis* (blue) and *Ruditapes philippinarum* (brown). Dashed lines represent 95% confidence intervals. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

species, had higher tolerance values at the lower end of the investigated temperature range, compared to *Ruditapes philippinarum*, an endobenthic species. However when the species-specific tolerance curves were compared to temperature forecasts specific for water and sediment, it was found that both species are likely to encounter high mortalities around the same decades. Furthermore, some differences could be seen between the mortality scenarios computed using the trend of water temperature forecast versus the full scenario which included hourly patterns. This shows the importance of micro-habitat modulation and is an indicator of the necessity to use habitat specific forecasts in order to avoid over- or underestimating risks.

Both species are regarded in the literature as “tolerant”, being able to tolerate a large range of temperatures and both have high potential for becoming invasive when arriving in novel areas (Breber, 2002; Lockwood and Somero, 2011). However, even if the range of temperatures that they could withstand is broad, the time they could spend at these temperatures before encountering a high mortality risk will be the limiting factor. This is different between the two species, especially for temperatures in the range of 25–28 °C, which *M. galloprovincialis* could withstand for longer periods. When paired with the habitat-specific forecasts, the differences in risk were limited, given that water temperatures reached and became risky at higher values (34 °C) compared to sediment temperatures (29.4 °C).

An important assumption that was made in this study was that any recovery time, even a very short one, would lead to ‘complete recovery’, thus every time the temperature dipped below each temperature tested, the consecutive hours above the tested temperature would reset to ‘zero’. There is an indication that daily fluctuations can have an impact on performance: generally, fluctuating temperatures that remain within a tolerable temperature range can improve performance, by contrast, those extending to stressful temperatures may have either positive or negative impacts (Colinet et al., 2015; Vajedsamiei et al., 2021), with high temporal variance causing the ability to mitigate impacts of rising mean temperatures due to climate change (Benedetti-Cecchi et al., 2006). Bai et al. (2019) found that night-time recovery temperature can be an important predictor of performance, however a literature search revealed that studies on recovery time are limited, and no information is available for the species here tested. It would be important to conduct follow-up laboratory experiments to investigate the appropriate recovery times and improve this model approach. Laboratory experiments would also be useful to refine these models with thresholds of tolerance from individuals for the specific area, rather than literature estimates from the native range. These individuals may already be used to the conditions, or be exposed to other chronic sources of stress that can act in a synergistic or antagonistic manner (e.g. Carneiro et al., 2021; Marigómez et al., 2017). This study only took adults into account, but the inclusion of multiple ontogenetic stages is necessary for better demographic projections, as juveniles may be more vulnerable (Truebano et al., 2018).

Fine-tuning these types of tolerance models is essential, not only to improve the ecological understanding, but also for resource management. Bivalve aquaculture is considered to be at a high risk from climate related changes: as shown by (Froehlich et al., 2018) the suitable area for farming these species is shrinking. The vulnerability of the sector is not only dependent on the climate change related exposure (to both temperature and other related stressors such as salinity increase; see Castro-Olivares et al., 2022; Des et al., 2021) and taxon-specific sensitivity but also on the adaptive capacity of the sector itself in face of these challenges (Stewart-Sinclair et al., 2020). Tolerance landscapes as intended in this study only take mortality as a risk index and use the

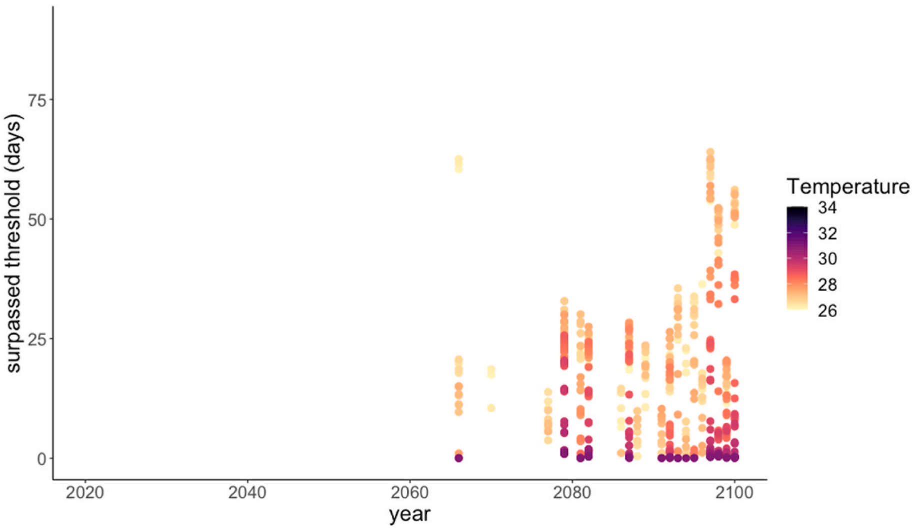

Fig. 5a. Number of days above mortality threshold for *Mytilus galloprovincialis* at different temperatures ranging from 26 °C (yellow) to the maximum recorded temperature (dark purple) for the whole study period 2020–2100. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

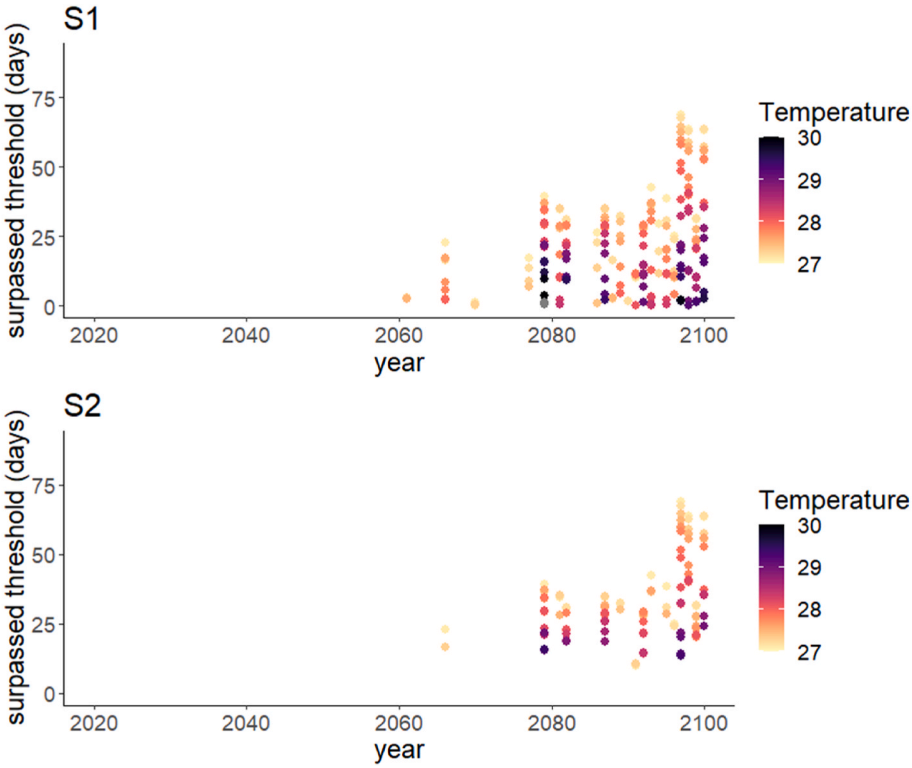

Fig. 5b. Number of days above mortality threshold for *Ruditapes philippinarum* at different temperatures at the two sites: S1 (coarser sediment) and S2 (finer sediment).

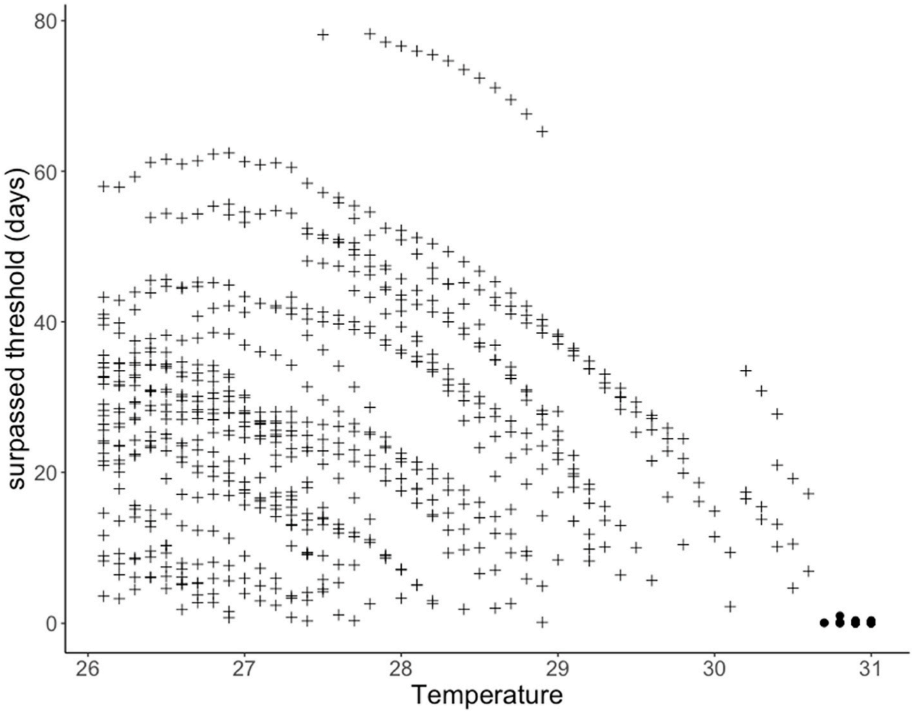

Fig. 6. Number of days above the mortality risk curve for *Mytilus galloprovincialis* (water) estimated by the trend (+) when the fluctuation did not exceed the threshold and by the fluctuations (dots) when the trend did not exceed it, for the whole temperature range and the whole period (2020–2100).

threshold of 50% mortality. However a 30% mortality could be already considered as an abnormal mortality (Soletchnik et al., 2007) and bivalve's mass mortality (MMBs) events have been defined on this basis as '*sudden loss (within 30 days) of more than 30% of the bivalve stock*' (Soon and Zheng, 2019). Furthermore, changes in growth and reproduction should also be considered as important indicators for the overall health of the sector. Understanding the onset of sublethal events or compensation of stress with behaviours (e.g., burrowing deeper, controlling valves opening) and the consequences of this for fitness and production, would be necessary (e.g. Vázquez et al., 2021). Another point that must be considered when looking at the results presented in this study is that between now and the end of the century, genetic adaptations could take place. Adding some dynamic to the tolerance landscape would be useful, provided that the decisions are supported by empirical studies. This is something that warrants further investigation with ad-hoc experimentation before inferences could be made for such long-term forecasts.

Only limited data sets were available for creating the scenarios, especially for the sediment temperature, where all information is drawn from one year of observations taken at five different sites. To obtain a reliable impression of the conditions in the sediment, data for multiple years at various locations would be necessary. Another limitation of this model is the assumption that temperature fluctuations within months stay relatively constant in the future. The model uses an estimate of the typical range of temperatures for each calendar month, which is based on current observations. Research such as the assessment by Coppola and Giorgi (2010) indicates that climate change could generally cause more extreme weathers especially in summer, thus also increasing the temperature range within the same month, a factor that should be taken into consideration when refining this method. Furthermore, it should be noted that sediment predictions were only done for one depth, whereas infauna can occur at different depths. Different species tend to have a preferred depth and the forecasts done in this study were targeted at the depth inhabited by *R. philippinarum*, which tends to be shallower than its counterpart *Ruditapes decussatus* (Macho et al., 2016). However, heatwaves themselves could elicit differences in burrowing behaviour (Domínguez et al., 2021; Zhou et al., 2022). An improvement to the model could be given by the addition of a diffusion coefficient, to be determined with empirical measurements at different depths that may enable making predictions for different target species.

5. Conclusions

Despite the above mentioned limitations, the results of the models, which are based on the worst case scenario (RCP 8.5) and predict the increase in the frequency of mass mortality events around 2070, is in line with predictions from both Froehlich et al. (2018) and Stewart-Sinclair et al. (2020) that predict the onset of decline for the bivalve mariculture sector from 2060, with tipping points in EU between 2060 and 2080, also based on the RCP 8.5 scenario (Stewart-Sinclair et al., 2020). Given that Italian production of clams accounts for 77% of total EU production (EUMOFA, 2022) and most of it is produced in the northern Adriatic lagoons, habitats which are characterised by daily temperature fluctuations, considering a loss of 50% of production based on average production in the last decade (2012–2021; Veneto Agricoltura, 2022) would lead to a loss of 15000 tonnes of produce or €75 million, of which €1.3 million come from the Venice Lagoon (based on 2021 price of €5/kg, EUMOFA 2022). To conclude, with this study we combined the tolerance landscape approach with forecasted scenarios, demonstrating that while species-specific tolerances are important, they should be considered within the framework of the microhabitat inhabited by each species. This approach may therefore give better estimates compared to those considering a stable environment that fail to consider the species habitat preferences.

Data statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:C. Bertolini, D. Glaser, M. Canu, R. Pastres reports financial support was provided by Provveditorato for the Public Works of Veneto, Trentino Alto Adige and Friuli Venezia Giulia provided through the concessionary of State Consorzio Venezia Nuova and coordinated by CORILA under the project Venezia2021.

Data availability

Data will be made available on request.

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