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Tolerance landscapes can be used to predict species-specific responses to climate change beyond the marine heatwave concept: Using tolerance landscape models for an ecologically meaningful classification of extreme climate events

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ABSTRACT

To predict the responses of organisms to changes in intensity and frequency of heatwaves, it is essential to gain a thorough understanding of how organisms respond to temperature exposure. Species-specific curves are more informative, yet more difficult to ascertain, than the generic heatwave definition (five days or more at a temperature above the 90% percentile) when addressing mortality risk and should be included when predicting thermal risks. The thermal tolerance of organisms is dictated by a combination of exposure intensity and duration: the aim of this study was to build a 'tolerance landscape' model, based on exposure thresholds to a potentially stressful temperature range, for the commercially important clam Ruditapes philippinarum using ten years of summer temperature time series in four lagoons in the Northern Adriatic, where this species is being commercially farmed. The model is based on a log-linear relationship between LT_{50} and exposure time. The two model parameters, i.e. the lethal temperature at 1 min exposure (CT_{max}) , and the temperature sensitivity parameter (z) were estimated on the basis of a systematic literature search. Best-fitting values, i.e. $CT_{max} = 54.5$ (± 2.3) and z = - 5.72 °C (± 0.66) are within the ranges found for other bivalves. Results show that the mortality threshold was exceeded for most lagoons in summertime in 2015, 2017 and 2018 suggesting that the risk of exceeding the mortality threshold is increasing, due to an increase in frequency and duration of extreme temperature events. Comparisons with the generic 'marine heatwave' definition showed that, while in some occasions 'heatwaves' occurred that were not risky for R. philippinarum, in one case the model identified a time period of mortality risk that would not have been classified under the generic 'heatwave' definition. These mismatches suggest that tolerance curves can be a good addition to productivity and site selection models, incorporating a metric of species-specific risk that can be used to predict the consequences of climate change on fishery and aquaculture, and can find their place in conservation and restoration toolkits for forecasting changes in habitat suitability under future climate scenarios.

1. Introduction

With ongoing climate change, extreme climatic events, such as heatwaves, are predicted to increase in frequency, intensity and duration (Oliver et al., 2019). For marine ecosystems, the definition of a heatwave is 'an anomalously warm event that lasts five of more days, with temperatures warmer than the 90th percentile (Hobday et al., 2016a)'. Generally heatwaves have been found to have deleterious effects on diversity and ecosystem services, but the effects varied considerably between different ecosystems and functions considered

(Smale et al., 2019). The current heatwave definition, however, cannot predict the specific impacts at the individual, species or population levels. The capacity of a given species to withstand high temperatures for a certain amount of time is related to its thermal tolerance: developing and testing thermal tolerance models is, therefore, of paramount importance for assessing the ecological consequences of 'heatwaves' and, perhaps, for providing a species-specific definition of 'heatwave' (Pansch et al., 2018; Smith, 2011; Sorte et al., 2010).

To predict the responses of organisms to changes in intensity and frequency of heatwaves, the use of critical thermal maxima as a baseline

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Received 20 July 2020; Received in revised form 5 February 2021; Accepted 11 February 2021 Available online 17 February 2021 0272-7714/© 2021 Elsevier Ltd. All rights reserved. against which to classify events as 'extreme' has been advocated (Galli et al., 2017). The thermal tolerance of organisms, however, is dictated by more than simply their critical upper thermal limits, as an organism's ability to withstand a certain temperature is inherently dependent on the time of exposure, which may also vary in relation to other stressors (Bigelow, 1921; Kingsolver and Woods, 2016).

Recent work on climate impacts has focused on developing theoretical models for thermal tolerance. Tolerance landscape theory (Rezende et al, 2011, 2014) provides a means of identifying species-specific critical thresholds based on both intensity and duration of stressing events. This theory assumes a log-linear relationship (Bigelow, 1921) between the temperature and the exposure time required to reach a 50% mortality rate (LT₅₀). Tolerance landscape models could be relevant in different fields of applied ecology and sustainable management of halieutic resources, such as habitat restoration and aquaculture. Methodologies for aquafarm site selection could also benefit from the inclusion of mortality thresholds (Brigolin et al., 2017; Porporato et al., 2020; Sicard et al., 2006). For example the use of 'seasonal forecasting' has been deemed useful for the management of fisheries and aquaculture, by combining it with biological habitat suitability data (Hobday et al., 2016b). These habitat suitability indices (Bayliss et al., 2005; Ovinlola et al., 2018) are currently 'static' and they may be enhanced by the inclusion of thermal tolerance models which include the temperature-time dynamics, something that would enhance their predictive power with respect to climate change scenarios.

The Mediterranean sea is highly vulnerable to climate change (Lejeusne et al., 2010), which is leading to an increase in the frequency, intensity and duration of heatwaves (Darmaraki et al., 2019a, 2019b). In this regard, model predictions indicate that the impact of extreme events could be more severe in the Northern Adriatic (Darmaraki et al., 2019b), leading to an increase in the risk of mass benthic mortalities (Di Camillo and Cerrano, 2015). Moreover, lagoons and other shallow water marine habitats may be more impacted than deeper areas due to thermal exchanges with air, leading to larger fluctuations in temperatures and higher temperatures overall compared to open sea likely to be observed (Amos et al., 2017; Brito et al., 2012). Therefore, in this study we focused on four Northern Adriatic Lagoons, which seem to be already experiencing the effects of global warming. For example, according to Kennish and Paerl (2010), water temperature increased and rainfalls decreased in the last 50 years in the Venice Lagoon. Shallow coastal ecosystems are also 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).

Ruditapes philippinarum, the Japanese Manila clam, is distributed widely in the Indian and Pacific oceans. Over the last 30 years it has been introduced along large parts of the European coastline, from the United Kingdom to the Mediterranean basin, becoming the main clam reared in Europe, where in certain areas it has an established wild population. The expansion of this clam has been facilitated by its biological traits, such as high fecundity, a long larval phase (ca. 3 weeks), broad salinity (15-50 PSU) and temperature tolerance (6-30 °C) (Breber, 2002). Current habitat suitability models developed for this species do not include water temperature (Vincenzi et al., 2007). Temperature, however, can be important to predict how species will cope with changing climate, in order to make informed decisions concerning management and, if required, relocation of cultivation areas (Galli et al., 2017). This is particularly useful in the case of a species showing a declining in stock which may be climate related (Ponti et al., 2017). The aim of this study was therefore to build a thermal landscape model for the clam R. philippinarum using tolerance landscape theory and investigate whether this method could be used to explain some of the recent mortality events and production losses.

2. Materials & methods

2.1. Model structure and parameter estimation

Following Rezende et al., 2014, thermal death curves can be obtained via the relationship between the temperature which leads to a 50% mortality rate (LT_{50}) and the exposure time which causes such mortality. The relationship between exposure time and LT_{50} is expressed by eq. (1) (Rezende et al., 2014)

$$T_{ko} = CT_{max} - zlog_{10}(t_e) \tag{eq.1}$$

Where: t_e is the exposure time (in minutes), T_{ko} is the LT₅₀, CT_{max} is the LT₅₀ within 1 min of exposure, and z is a constant that characterizes the sensitivity to temperature change.

The model parameters were estimated 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. The Goodness of Fit was assessed by plotting the standardised residuals to visually check assumptions of homoscedasticity and normality of residuals. The visualisation was coupled with Shapiro test, autocorrelation of residuals and checking that sum of residuals equal zero. The model was then cross-validated using the Leave-One-Subject-Out method ('LOOCV', package *caret* version 6.0–86 in R). The output of the model is a time of exposure-temperature tolerance curve with 95% confidence intervals that can be used to compare with temperature observations for a given period.

Data for parameter estimation were searched as follows. Web Of Science was used for literature searches with the species names (Ruditapes philippinarum OR Venerupis philippinarum OR Venerupis semidecussatus OR Venus philippinarum OR Tapes philippinarum OR Tapes japonica OR Manilla clam OR Philippine clam) AND Thermal tolerance, species names AND Temperature tolerance, species names AND Lethal temperature, species names AND LT50. Papers presenting information on the lethal temperature, the mortality rate and the time of exposure to lethal temperatures were selected. Studies on survival in air and air temperature where excluded. If the LT₅₀ (temperature to 50% mortality) was not explicitly mentioned in writing, it was extracted from the survival curves presented in the graphs. To avoid confounding ontogenetic factors, only studies of adults were included. Six papers matching these criteria were found (Anacleto et al., 2014; Shin et al., 2000; Tobai and Miyama, 1995; Yang and Ding, 2012) Within these, Anacleto et al. (2014) used a fast ramping rate assay (1 °C/30 min) and another (Shin et al., 2000) used three slower rates (1 °C/day, 2 °C/day and 3 °C/day). The other ones presented the results of studies carried out at constant temperature (see Table 1 for further details on the selected studies). Furthermore, a similar search on Google Scholar, led to include a conference poster presentation (Rato et al., 2018). The literature search allowed the collation of 16 data points, which were used for estimating the parameter of the model. The range of methodologies used in the selected studies, with a range of acclimation temperatures and ramping rates negates issues raised by Rezende et al. (2011) and Santos et al. (2012) on the estimation of CT_{max} from ramping assays.

2.2. Model application

The model developed using the literature data arising from laboratory studies was then applied using temperature time series recorded *in situ*. Exposure times with respect to water temperature were estimated assuming that the time series recorded at each station, in the water column, were good proxies of the temperature at farm sites located in the proximal area. Details of the location of the sites and time series are summarized below. Summer temperatures ranges were sliced using a 0.1 °C step, starting from the lower stress temperature (27 °C, Tobai and Miyama, 1995) up to the maximum recorded temperature for each site (which was up to 34 °C). The number of consecutive hours in which the

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Table 1

Details of methodologies employed by the studies here considered.

Study	Region	Size of clams (mm)	Temperatures tested (°C)	Time	Method
Macho et al. (2016)	Spain (Atlantic)	42.1 ± 1.3	27, 32, 36	6–10 days	Tidal beakers heated. Ramped for 5 h 50 min to initially reach the desired temperatures @1.5,2.3 and 3 $^{\circ}$ C/h Mortality every 1–2 h
Anacleto et al. (2014)	Portugal	$\textbf{35.3} \pm \textbf{3.0}$	>22 up to LT50	<1 d	Ramping assay 1 °C/30 min
Yang and Ding (2012)	China	-	35,36, 38,40,42		Constant T immersions
Shin et al. (2000)	Korea		>18 up to LT100 >25 up to LT100		Ramping rates of 1 $^\circ\text{C/day},$ 2 $^\circ\text{C/day}$ and 3 $^\circ\text{C/day}$
Isono et al., (1998)	Japan	11.4–16.7	10–34	4 weeks	Constant temperature
Toba Myiama	Japan		10, 17, 23, 27 (experiments 1	2–3	Acclimated to experimental temperatures by 2–3 $^\circ\text{C}/\text{day}$ and then left
(1995)			& 2)	months	exposed
			16,19,23,27 (experiment 3)		
Rato (2018) (poster)	Portugal		5, 15, 20, 23, 26, 29, 32, 35	120 h	Constant temperature

water temperature remained above each value (e.g. above 27 °C, above 27.1 °C, above 27.2 °C etc) were counted. The longest record for each summer was taken as the 'exposure time' associated to a given temperature (see example in Fig. 1). For each temperature the difference between 'exposure time' and the lower confidence bound of the lethal threshold time predicted by the model, was taken as a proxy of the mortality risk. The maximum value for any given site and year was then selected as mortality risk index, rendering it independent of temperature

at which this surpassing occurs. Positive values mean that clams spent a given number of days at temperatures for which the model predicts a risk of mortality for at least 50% of the population, at a 95% confidence level: the higher the value, the riskier. Any negative value represents years-site combination with no risk of LT_{50} .

The methodology, as explained above, was then applied to four Northern Adriatic lagoons (see Fig. 2), where *Ruditapes philippinarum* is farmed: Venice, Scardovari, Marinetta and Marano. In these lagoons,



Days since beginning of summer

Fig. 1. Example of model testing for one site (ve-1). The time series represents the complete summer of 2015. The blue dots represent consecutive hours of exposure at the specified temperatures, respectively 28.8 °C (red) and 30.8 °C (dark red) for the same summer. ET indicates the longest exposure for each summer which was selected as the Exposure Time. The black horizontal line represents the lower confidence bound of threshold from the tolerance landscape model. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)



Fig. 2. Map of the study lagoons located in the North West Adriatic Sea. Insets represent the four lagoons here investigated; the triangles represent the locations where temperature was recorded.

environmental water data (Temperature, Salinity, Oxygen, Turbidity and Chlorophyll-a) are collected every thirty minutes using automatic probes by public monitoring networks managed, respectively, by Provveditorato Interregionale per le Opere Pubbliche per il Veneto, Trentino Alto Adige e Friuli Venezia Giulia, Ex Magistrato alle Acque – Venezia, for the Venice lagoon, and the Environmental Protection Agencies of Veneto and Friuli Venezia Giulia for the lagoons of Scardovari, Marinetta and Marano. The data from Venice were made available upon request. Data for the other lagoons were open access and downloadable (https://www.arpa.veneto.it/dati-ambientali/open-data/idrosfera /acque-di-transizione/acque-di-transizione-boe-delta-del-po;

http://www.arpaweb.fvg.it/bs/gmapsbs.asp). Three monitoring stations from a network in the Venice lagoon were selected, based on their location near clam farms (Pessa et al., 2018) in the southern (Chioggia (ve-10): N 45° 12.68446, E 12° 14.54917'), central (Fusina (ve-1): N 45° 28.14261' E 12° 20.10500') and northern (Campalto (ve-2): N 45° 24.73918', E 12° 16.44823') part of the lagoon (see Fig. 2), data were available from 2008 to 2018. The lagoons of Scardovari (N 44° 53.58621 E 12° 26.31055) and Marinetta (N 45° 3.312547' E 12° 20.56867') are located in the delta of the river Po, therefore, in general, are characterized by a higher primary production, fuelled by the dissolved inorganic nutrients carried by the river. Data from these lagoons were available for the period 2010-2018. The lagoon of Marano is the northernmost one: from the number of buoys in the monitoring network, the one closest to the cultured area was chosen (from Sladonia et al., 2011; N 45° 43.34795 E 13° 8.091144), where we had data from 2013, 2017 and 2018. The average depth of the probes, as measured by pressure sensors (where available), of these monitoring stations was 60 \pm 30 cm, with the minimum recorded depth of 10 cm and the maximum of 200 cm, given by tidal fluctuations. It should be noted that these temperatures represent water temperatures at the site and not the sediment temperature, however at the shallow sediment depth inhabited by clams water and sediment temperatures are similar.

These same time series of summer water temperatures were also processed in order to determine the heatwave threshold, i.e. the 90th percentile of the distributions for each station. The number of consecutive hours above threshold (then transformed in days) was used to estimate the number of marine heatwaves following the 'classical' definition, i.e. events in which water temperature exceeded the threshold for five consecutive days (Hobday et al., 2016).

All of the time series analyses were performed in R version 3.6.3 (R Development Core Team, 2020).

3. Results

3.1. Parameter estimation

The parameters *z* and *CTmax* were estimated as described in section 2, obtaining the following values: z = -5.72 °C (±0.66), $CT_{max} = 54.5$ °C (±2.3). The residual standard error was 2.25 °C. The thermal death time (TDT) curve is shown in Fig. 3. The model explains a significant fraction of the total variance (df = 14, Adj. R² = 0.83, p < 0.0001).

3.2. Exposure time and mortality risk

Descriptive temperature statistics for the six stations are described in Table 2.

In order to identify events characterized by a high risk of mass mortality, observed exposure times were compared with the 'tolerance threshold' predicted by the model (in Fig. 4). The comparison between the observed exposure times at stressful temperatures and the tolerance threshold predicted by the model indicates that the risk of mass mortality was highest in 2015, when the threshold was exceeded in the Venice Lagoon and 2015, 2017 and 2018 in the Scardovari and Marinetta Lagoon (Table 3). In the Marano lagoon no 'heatwave' was recorded, but in 2018 there was an exceeding of 'tolerance time' for temperatures lower than the upper 90th percentile.

Fig. 5 summarises the findings. From this figure it can be seen that 2015 and 2018 were stressful years, in which the threshold was surpassed in at least some of the sites. The worse years were 2015 in



Fig. 3. Thermal Death Time curve for Ruditapes philippinarum. Black dots represent data extracted from the literature. Red part of the line represents the temperature range considered in this study, dashed red lines are the lower and upper confidence intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 2

Minimum, median and max summer temperatures recorded at each station. The consecutive number of days above heatwave threshold, which was identified at 29.2 \pm 0.5 °C are presented in Table 3.

Station	Min T (°C)	Median T (°C)	Max T (°C)	
Ve-1	15.69	26.38	33.31	
Ve-2	14.26	25.48	33.31	
Ve-10	13.39	26.03	34.12	
Scardovari	18.22	26.64	32.84	
Marinetta	17.8	25.69	31.2	
Marano	13.84	25.8	32.3	

Scardovari (12.37 days) followed by 2018 in Marano (9.76 days) and Scardovari (7.87 days). In 2015 ve-2 site was very closed to reaching the risk threshold (-0.42 days) and in 2017 the Scardovari lagoon also approached the mortality risk threshold (-0.28 days).

4. Discussion

This study aimed at building a tolerance landscape model (*sensu* Rezende et al., 2014) for the Manila clam *Ruditapes philippinarum* and apply that to hindcast mortality risk. Model parameters were estimated on the basis of a thorough literature analysis and the model was applied to six decadal water temperature time series, collected in four Northern Adriatic lagoons. The results show that events that are classed as 'heatwaves' do not always match 'risky' conditions for *R. philippinarum*, because a prolonged exposure at temperature lower than the 90th percentile can be risky for some organisms. Moreover, the frequency of

risky events is increasing, and this could pose severe threats to the farming of this species in near future.

The thermal tolerance parameters of *R. philippinarum* are consistent with the values presented in Rezende et al. (2014) for bivalves (z ranging from 3 to 7 °C and CT_{max} from 35 to 50 °C). In principle, z and CT_{max} are tightly associated as species with a high CT_{max} usually present a high z (Rezende et al., 2014), which suggests that the ability to withstand extreme temperatures, encapsulated in CT_{max} , cannot be sustained during long periods of time, as evidenced by higher values of z. Our estimate of CT_{max} for R. philippinarum is slightly higher compared to that for other bivalves, but the z value lies within the range given above. Species with high CT_{max} and low z are less sensitive to temperature changes, tolerating high temperatures for longer amount of time. This suggests that R. philippinarum is indeed a tolerant species (Moschino, 2007) which can withstand large temperature fluctuations in transitional lagoon environments. Despite this higher tolerance, there was a decline in clams production recorded in the northern Adriatic Lagoons in the recent years (e.g. in the Venice lagoon since 2015, Pessa et al., 2018). Comparing 2017 with 2010, there was an regional loss of production of 28.6%, and just within the Venice Lagoon this loss can be estimated at 20% per year (Severini and Liviero, 2019). These losses are probably related to the synergic action of several potential environmental stressors: beside temperature, which was the main focus of the present study, hypoxic conditions and salinities close to the tolerance range of this species may play a role, particularly in complex lagoon ecosystems.

Climate change, which is already causing rising temperatures, may play a role in the loss of aquaculture productivity of the Adriatic (Rodrigues et al., 2015). The effects of climate change on settlement of clam larvae in the Venice lagoon was investigated in (Ghezzo et al.,



Fig. 4. Points representing exposure time above each temperature as recorded for each sensor in Venice, Scardovari, Marinetta and Marano Lagoons. Colours are the years where environmental data were available. Continuous black line represents tolerance threshold for adults R. philippinarum and segmented lines represent 95% confidence intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 3

Number of consecutive days (calculated from the number of hours) above the upper 90th percentile of summer temperature for each station. For every summer it is indicated whether this would be classified as a heatwave (yes) or no (no). N/A represents years where complete summer was missing for the specific location. Asterisk (*) are placed for the years in which mortality risk for R. philippinarum was identified from the tolerance landscape model.

	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
Ve-1	0.6 (No)	0.6 (No)	N/A	4.46 (No)	N/A	1.79 (No)	N/A	7.94 * (Yes)	2.79 (No)	N/A	9.71 (Yes)
Ve-2	0.58 (No)	0.6 (No)	2.9 (No)	0.87 (No)	0.81 (No)	N/A	0.29 (No)	8.72 (Yes)	1.73 (No)	3.56 (No)	N/A
Ve-10	0.64 (No)	0.79 (No)	N/A	2.71 (No)	N/A	0.87 (No)	N/A	3.81 (No)	2.23 (No)	5.43 (Yes)	N/A
Scardovari	N/A	N/A	3.31 (No)	6.44 (Yes)	1.44 (No)	0.87 (No)	0.77 (No)	10.8* (Yes)	3.54 (No)	6.58* (Yes)	7.23* (Yes)
Marinetta	N/A	N/A	4.02 (No)	1.79 (No)	0.33	1.94 (No)	0.15 (No)	0.03 (No)	0.81 (No)	4.81 (No)	14.48* (Yes)
					No						
Marano	N/A	N/A	N/A	N/A	N/A	1.31 (No)	N/A	N/A	N/A	1.52 (No)	1.54* (No)

2018) using a reaction-transport model. The results highlighted the role of rising temperatures for the timing of the settlements, with scenarios based on IPCC for 2100 showing an anticipation of the typical summer settlement from August to May-July, and new spawning events occurring in October and November. Despite an increase in number of events, they found that the absolute quantity of settled larvae diminished. Moreover, the spatial distribution of settlement areas shifted. With climate change scenarios, the importance of temperature as a cause of mortality of young clams increased, with temperature leading to an increase of 22% in larval mortality in the 2100 IPCC scenario (Ghezzo et al., 2018). Climate was also pinpointed as the culprit of low clam production in 2003, year in which an exceptional heatwave was recorded (Ponti et al., 2017). The analysis of the water temperature time series shows that the heatwave threshold found for all stations (29 °C) is higher than the lower lethal threshold temperature for this species found in the literature (27 °C). In our study sites, as one can see in Table 3, three of the most recent years (2015, 2017 and 2018) experienced a heatwave in at least some of the stations but were not deemed risky for *R. philippinarum*, highlighting that not all of the events falling under the 'heatwave' definition can be considered stressful years for this species. The opposite is also true: in 2018 in Marano there was a risk of adult mortality due to a long period at a stressful temperature lower than the heatwave threshold. These examples of mismatches show how using an approach based upon the general heatwave definition (Caputi et al., 2016; Smale et al., 2019) may not be appropriate, when physiological responses to change are different between species (Helmuth, 2009). Moreover, dealing with a non-native species, that originates from an area with a different climate and likely to have a thermal tolerance that exceeds a definition of stress based upon upper quantiles of previous decades in the non-native range, is something to consider in the context of mismatches between heatwaves and tolerance landscape risk. For example, native seaweeds were found to be more susceptible to heatwave stress compared to non-native (Atkinson et al., 2020). Since many species used in aquaculture can be considered non-native (e.g. at least 27 in Europe, Savini et al., 2010), it would be even more appropriate to identify thresholds based on their physiology rather than on climatological indices.

Limited mortality data were available to corroborate the findings from the tolerance model here presented. However, a general pattern could be seen as the stressful years matched in the different sites (as all shallow coastal lagoons are in the similar geographic area) and these also matched some of the reported mortalities, obtained from the available observations of 2014–2018 (Arcangeli G., Pers. Comm.), especially in 2017 and 2018. In 2018 there was a high summer adult mortality reported in Marinetta that is in accord with the temperature stress reported in this model. The year 2015 was also identified as a



Fig. 5. Mortality risk index expressed as number of days away (points) from the lethal threshold (represented by the horizontal line, at day 0) for each year and station (colours). Points below the dotted line are negative numbers and represent site-year combinations where the threshold was not reached, the lower the number the longer exposure necessary to reach mortality. Points above the line (positive numbers) represent stations where such threshold was surpassed, the higher the number the longer exposure above threshold experienced. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

critical one, characterized by a dry and warm summer, with air temperatures in July exceeding the long-term average temperatures values by 3 °C and in August and September by 1.5 °C (ARPAV, 2016). This was found critical for aquaculture, which saw great losses (e.g. up to 5000 tonnes of clams lost from the Goro lagoon, Bartoli et al., 2016) and news reporting high mortalities for fish and clams in most of Italy (Licci, 2015), matching up with the exceeding temperature tolerance here reported for the Venice lagoon. Some of the other years when 'anomalous mortality' was recorded were not fully explained by the model. In Chioggia for example, in 2017 an 'anomalous mortality' event was recorded at the end of the summer period (September) but according to the thermal tolerance model here presented, the threshold was not surpassed. However, the mortality reported was 25%, thus below the 50% limit that was used to build the model, and it can be seen that in this site during 2017 the lagoon water was at 29.4 °C for a period which was within 24 h of the threshold line. The model here used assumes that the periods in between consecutive events are enough for recovery. In reality, stress can be accumulated (Pansch et al., 2018), repeated stressors may limit species tolerance (Seuront et al., 2019) and the total number of hours above stressful temperatures may lead to identify different years as 'stressful'. Before making further inferences, it is however necessary to obtain data on the recovery time needed by this species, which is currently lacking. Moreover, the model here used refers to adult lethal thresholds, something that may also contribute to the mismatches. Clams are generally seeded in spring in Adriatic lagoons, which can place younger individuals at greater risk of heat stress (G.R.A.L., 2006). Overall a better record of mortalities combined with more laboratory studies on different life stages could help disentangling the vulnerability to stress of different cohorts and their response to the presence of co-stressors, improving the present model and driving better seeding practices.

The method used in this study used temperatures recorded in the water column. It is worth noticing that *R. philippinarum* and other benthic organisms inhabiting soft-bottom habitats, are exposed to sediment temperatures that may differ from water column ones. A model of sediment temperatures in the Venice lagoon shows that sediment temperature in summertime is cooler than water temperature during the

central hours of the day while at night and morning is similar. Moreover, in the top layer (< 25 cm) appears to be similar to water compared to deeper where is cooler. Laboratory experiments also show that sediment temperature results stratified becoming lower in the deeper layers (e.g. 2 cm vs 7 cm, Macho et al., 2016). Behavioural responses to high water temperatures can result in deeper or long-time burrowing to escape the stressor, as and different species have different burrowing depths (e.g. Ruditapes decussatus burrowing down to 8 cm, whereas R. philippinarum staying at shallower depths around 3 cm, Macho et al., 2016). Staying shallower may thus lead to exposure at higher temperatures. This behaviour can lead to secondary stressors, such as lack of feeding time and the necessity of switching to anaerobic metabolic pathways. The role of microhabitat temperature, driven by structure, colour, shape and other micro-properties of the habitat moreover, is increasingly present as a subject of climate change research (Monaco et al., 2016; Scheffers et al., 2014), and it could be a useful integration to future developments of this model, as for example sediment properties are spatially heterogeneous.

Temperature is not the only stressor to which R. philippinarum is vulnerable: other causes of mortality have been identified, such as the parasite Perkinsus olseni, changes to salinity, oxygen and ocean acidification. Before analysing these causes in further details it is worth noting that these are also inherently related to weather, temperature and thus to climate change (e.g. Jeppesen et al., 2015; Miyamoto et al., 2019), rendering it easy to confound these with temperature effects, the focus of this study. Perkinsus olseni is a parasite that is able to cause massive mortality of clams. Environmental factors such as warm temperature (20-25 °C) and high salinity are reported as accelerators of the development of P. olseni in Manila clams (Cigarría et al., 1997) but high levels of infections are usually reported for the autumn-winter months, while are lowest in the summer months (Jasim Uddin et al., 2010). It is therefore more likely that autumn mass mortalities can be related to P. olseni infections, such as that recorded in the Venice lagoon in autumn 2011 (Pretto et al., 2014). It has to be noted that the frequency of infections from this parasite is increasing (Arcangeli, 2017) and it may be also a factor related to climate change that should be investigated. An additional factor highly cited in literature as a cause of R. philippinarum mortality is salinity. This species is tolerant to high salinities (35-42 g/L) while it is vulnerable to low salinities (0–7 g/L) which are a lead cause of mortality (Carregosa et al., 2014). In shallow lagoon ecosystems like those investigated in this study, salinity fluctuations are strongly linked to temperature and precipitation regimes, from processes of evaporation and large amounts of freshwater inputs. In the areas investigated in this study, low salinities occurred mostly during autumn, winter and spring periods (Supplementary Table 1), thus not explaining summer mortalities. Nonetheless, these occurrences may explain some of the high mortalities that have occurred outside of the summer months (Humphreys et al., 2007). While oxygen limitation is usually considered as an issue for many species, moderate or short-term hypoxia does not threaten the survival of R. philippinarum (Li et al., 2019). However, interactions between oxygen and temperature should be investigated to improve the tolerance curve to accommodate multiple potential stressors, as low oxygen levels are usually recorded in summer periods (Supplementary Table 1), Evolutionary adaptations to climate are likely to happen (Bush et al., 2016), but it must be noted that current practices of clam culture involve importing seeds from abroad, which would not allow for such acclimation, thus this was not accounted for in the study here presented.

In conclusions, the tolerance landscape model framework may be used as a simple tool to model thermal tolerance as a function of both temperatures and time, making it possible to use as a site and speciesspecific approach, creating 'site suitability' scenarios. This can be extremely important in the context of adaption to climate change (Oyinlola et al., 2020) For example, the results of this study suggest that the in the last decade the risk of summer mass mortality has increased in most of Norther Adriatic lagoons, in some sites more than others. Mass mortality is an issue both economical and of sustainability, wasting the initial resource (seed) and having a lower return from the initial investment. This model can be therefore paired with scenarios of future temperatures, which should be provided in a spatially explicit and ideally site-specific format (Falconer et al., 2020), given that lagoons will not respond linearly to change (Brito et al., 2012). The findings could be then used to plan the allocation of new leased areas, to ensure their suitability in terms of lower risks. Similarly they can be used to update yield models for these areas (e.g. Vincenzi et al., 2011) which should include mortality risks as a function of temperature exposure in time. This latter addition can help ensure maximum returns are obtained for the amount of resources invested and be of high value for site selection tools.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2021.107284.

CRediT author statement

CB- Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Writing- review & editing, Visualization.

RP- Conceptualization, Methodology, Resources, Writing- review & editing, Visualization, Supervision, Project administration, Funding acquisition.

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