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Current and future thermal habitat suitability of the European clam *Ruditapes decussatus* (Linnaeus, 1758) in Mediterranean coastal lagoons

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ABSTRACT

The European clam *Ruditapes decussatus* contributes to ecosystem functioning and supports fisheries in coastal lagoons across the North-Eastern Atlantic and Mediterranean. Although the ecological consequences of climate-driven warming in lagoon systems are increasingly documented, its implications for the spatial distribution and habitat suitability of benthic species remain poorly understood.

To address this gap, we quantified the metabolic response of *R. decussatus* across a wide range of temperatures (8-38 °C) by measuring respiration rate (RR). RR increased with temperature, from low values at 8 °C (0.07 ± 0.04 mg O_2 h^{-1} g^{-1} DW) to a maximum around 26 °C (1.55 ± 0.40 mg O_2 h^{-1} g^{-1} DW), followed by a sharp decline at higher temperatures. Among 24 candidate Thermal Performance Curve (TPC) models, the best-fitting function indicated an optimal temperature of 26.7 °C and a critical thermal maximum of 38.0 °C.

TPC-derived parameters were then used to generate seasonal maps of Thermal Habitat Suitability (THS) under reference conditions (2017-2022) and future climate warming scenarios (RCP 4.5 and RCP 8.5 for 2050) across four Mediterranean lagoons. Under reference conditions, THS showed seasonal and spatial variability, with highest suitability during summer and early autumn and lower values in winter.

Future projections indicate a seasonal reshaping of habitat suitability, with increased values during winter, spring, and autumn, and a moderate decline during summer (up to 4% under RCP 8.5). Climate warming may therefore reshape the reproduction timing of the species, with implications for population dynamics and ecosystem functioning. Integrating THS into management frameworks may support future aquaculture and conservation planning.

1. Introduction

The Mediterranean Sea, among the seas most vulnerable to the effects of global climate change, is experiencing faster water warming than the other seas and oceans (Giorgi and Lionello, 2008; Cramer et al., 2018; IPCC, 2023). Since 1982, the Mediterranean Sea surface temperature (SST) has been warming at a rate of 0.4 °C per decade (Pastor et al., 2020; Pisano et al., 2020), and this trend is likely projected to increase throughout this century (Soto-Navarro et al., 2020). Warming waters are concurrently increasing the frequency of extreme events such as heatwaves, storms and flashfloods, representing a major threat to aquatic ecosystems and human livelihoods (MedECC, 2020; Oliveira et al., 2022; Ali et al., 2022). These episodic events are conceivably even more concerning when hitting coastal lagoons. Coastal lagoons are shallow bodies of water, partially separated from the sea by physical barriers (sandbanks, shingle or, less frequently, rocks), and connected at least intermittently to the open sea through one or more restricted inlets (Cataudella et al., 2015; Newton et al., 2018). These ecosystems provide distinct and valued socio-economic services and ecosystem functions, like water purification, flood regulation, microclimate stabilization, soil erosion prevention, biodiversity conservation and blue Carbon storage (Newton et al., 2014, 2018; Mitsch et al., 2015; Palmas et al., 2025). Due to their shallow depths, a limited hydrodynamism, short water turnover time, and limited ability to buffer the effects of rising air temperatures, coastal lagoons are particularly vulnerable to global warming (Ferrarin et al., 2014, 2024; de Vicente, 2021; Soulié et al., 2023), making them

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sentinel systems of ongoing changes (Eisenreich, 2005). For instance, climate-change related rising temperatures can have severe impacts on coastal lagoon biodiversity and trophic webs structure and performance (Vidussi et al., 2011; Pulina et al., 2016; Courboulès et al., 2022), on lagoons' sediment biogeochemistry (Sarà et al., 2021; Palmas et al., 2025), as well as foster the occurrence and spread of invasive allochthonous species and pathogens (Villalba et al., 2005; Rahel and Olden, 2008; Kordas et al., 2011; Robinson et al., 2020). Moreover, the increase in lagoons' water temperature can also support the proliferation of harmful algal blooms, which have cascading effects on food webs, the economy of local fisheries and the overall ecological health of the lagoons (Al-Wardy et al., 2025).

In the case of benthic invertebrates like mollusc bivalves, generally characterized by limited mobility, the tolerance to thermal extremes is higher than in most other benthic fauna (Helmuth et al., 2002). Nonetheless, extremely high temperatures can have strong impacts on these animals, disrupting their physiological homeostasis, leading to oxidative damage, impaired cellular survival, and metabolic imbalance (Costa et al., 2020; Lam-Gordillo et al., 2025; Papadopoulos et al., 2025). According to the oxygen- and capacity-limited thermal tolerance hypothesis, once temperature increases beyond an organism's optimum limits, it leads to a mismatch between oxygen supply and demand in the tissues (Pörtner, 2012). This mismatch can cause a progressive decline in performance, a compensatory transition from aerobic metabolism to partial anaerobiosis, and energy deficiency (Pörtner and Knust, 2007; Pörtner et al., 2017). These metabolic shifts might lead to energy reallocation from biomass production (including growth and reproduction) and activity to basal maintenance, which allows the temporary survival of the organism exposed to stressful conditions but negatively affects their fitness, feeding behaviour, growth and locomotion (Sobral and Widdows, 1997; Pörtner and Knust, 2007; Han et al., 2008; Pörtner, 2012; Rato et al., 2022; Plumlee et al., 2024). In addition, thermal stress can delay bivalves time burrowing time and reduce burrowing depth, thereby increasing the risks of predation and mass mortality under exceptionally elevated temperature (Archambault et al., 2014; Domínguez et al., 2021; Cui et al., 2025).

On the other hand, several studies have also shown that repeated exposure to sublethal thermal stimuli can modulate the organism's response to future environmental stressors. This modulation may occur through the acquisition of a form of stress memory, enabling the organism to tolerate changing conditions via phenotypic plasticity (Kang et al., 2016; Georgoulis et al., 2022; Alma et al., 2024), or, in the longer term, through adaptive genetic variation within the population (Delorme et al., 2024). This rapid and beneficial physiological response is known as "heat-hardening" and refers to the transient increase in thermal tolerance following brief exposure to sublethal temperatures (Bowler, 2005). Heat hardening can promote the development of phenotypes that are more resistant to thermal stress, often mediated by mechanisms such as the upregulation of heat shock proteins, improved cellular homeostasis, or enhanced metabolic efficiency (Sørensen et al., 2003; Bowler, 2005).

One of the most commonly used methods to assess how species respond to temperature changes is based on experimental estimates of their thermal performance through the modelling of Thermal Performance Curves (TPCs) (Angilletta et al., 2010; Sokolova et al., 2012; Kontopoulos et al., 2024). Bivalve mollusks are, indeed, highly sensitive to rising temperatures because their metabolism is directly dependent upon oxygen supply, which decreases at high temperatures. Indeed, oxygen consumption rate is the most widely recognised and effective proxy for the study of aquatic invertebrate metabolic activity (Pörtner, 2001; Pörtner et al., 2017). Oxygen consumption typically exhibits a bell-shape relationship with temperature (Sokolova et al., 2012; Pörtner et al., 2017). The position, skewness, shape, and heights of the TPCs define altogether a species' ability to respond to environmental fluctuations, providing a synthetic definition of some ecological traits (Sokolova et al., 2012). For instance, TPCs with right-positive skewness indicate cold thermal preference, left negative skewness is typical of heat-tolerant species and TPC symmetry is generally observed in generalist species (Angilletta et al., 2010; Sarà et al., 2013).

The performance responses to temperature changes have been widely used to predict spatial habitat suitability of several native and invasive fish, native mussels, invasive crabs and invasive clams (Cucco et al., 2012; Marras et al., 2015; Bosch-Belmar et al., 2022a, 2022b; Marchessaux et al., 2022, 2024; Johnson et al., 2025). The native bivalve *R. decussatus*, a common component of the benthic communities in Sardinian coastal lagoons (Cannas, 2010; Cabiddu et al., 2014; Cataudella et al., 2015) is a filter-feeding organism, thus contributing to mitigate local eutrophication (Coelho et al., 2002). Moreover, it is a local traditional resource of lagoon fisheries, and holds significant commercial value across Mediterranean coastal lagoons, as one of the most economically important mollusks (Marino et al., 2009; Cataudella et al., 2015).

Information on the effects of rising temperature on the habitat suitability of the European clam *Ruditapes decussatus* is, to the best of our knowledge, currently lacking. To contribute to fulfilling such a knowledge gap, we (1) estimated how changes in water temperature influence the physiological performance of *R. decussatus* and (2) modelled its thermal habitat suitability (THS) by comparing a reference period (2017-2022) with two projected future climate scenarios in four Sardinian coastal lagoons. We hypothesized that *R. decussatus* exhibits relatively high thermal tolerance and that future warming may lead to a seasonal redistribution of thermal habitat suitability, with changes in suitability across seasons and among lagoons.

2. Material and methods

2.1. Study area

The four lagoons considered in this study are distributed along the Sardinian coast (Italy) and cover a total surface area of about 32 km^2. They include the lagoons of Santa Gilla, Marceddì, Calich and Tortolì (Fig. 1).

The Santa Gilla Lagoon (ca.1300 ha) is the second-largest coastal lagoon of the island and is connected to the Gulf of Cagliari (Tyrrhenian Sea) through a single inlet. Freshwater inputs derive mainly from the Flumini Mannu di Cagliari and Rio Cixerri rivers (Atzori et al., 2018). Located between the historical and industrial ports of Cagliari, the lagoon has long been exposed to intense anthropogenic pressures. Despite this, it has high conservation value, being designated as a Special Protection Area, a Ramsar wetland, and a Site of Community Importance, and it also supports aquaculture of commercially important bivalves (Cabiddu et al., 2014; Culurgioni et al., 2015).

The Marceddì Lagoon (ca. 600 ha) consists of an outer basin connected to the sea and an inner basin influenced by freshwater inputs. In recent decades, strong anthropogenic pressure, associated with nutrient enrichment and reduced freshwater inflow, has triggered recurrent dystrophic crises and mass mortality events of benthic communities and fish (Murenu et al., 2004; Magni et al., 2005, 2008). The lagoon is designated as a Ramsar wetland and a Site of Community Importance and supports traditional fisheries.

The Calich Lagoon (ca. 92 ha) is connected to the sea through the Fertilia Channel, a natural inlet enlarged during land-reclamation works, although water exchange is limited by the lagoon's elongated morphology. Freshwater inputs derive from two natural tributaries and one artificial channel and are affected by industrial and domestic discharges. The surrounding catchment is largely agricultural, and the lagoon supports traditional fisheries.

The Tortolì Lagoon (ca. 250 ha) consists of an ovoid basin connected to the sea by two channels and receives freshwater mainly from the Rio Mannu. The system is characterized by sandy-muddy sediments and extensive seagrass meadows, mainly *Zostera noltei* (Giampaoletti et al., 2023). The lagoon supports long-standing traditional fisheries and

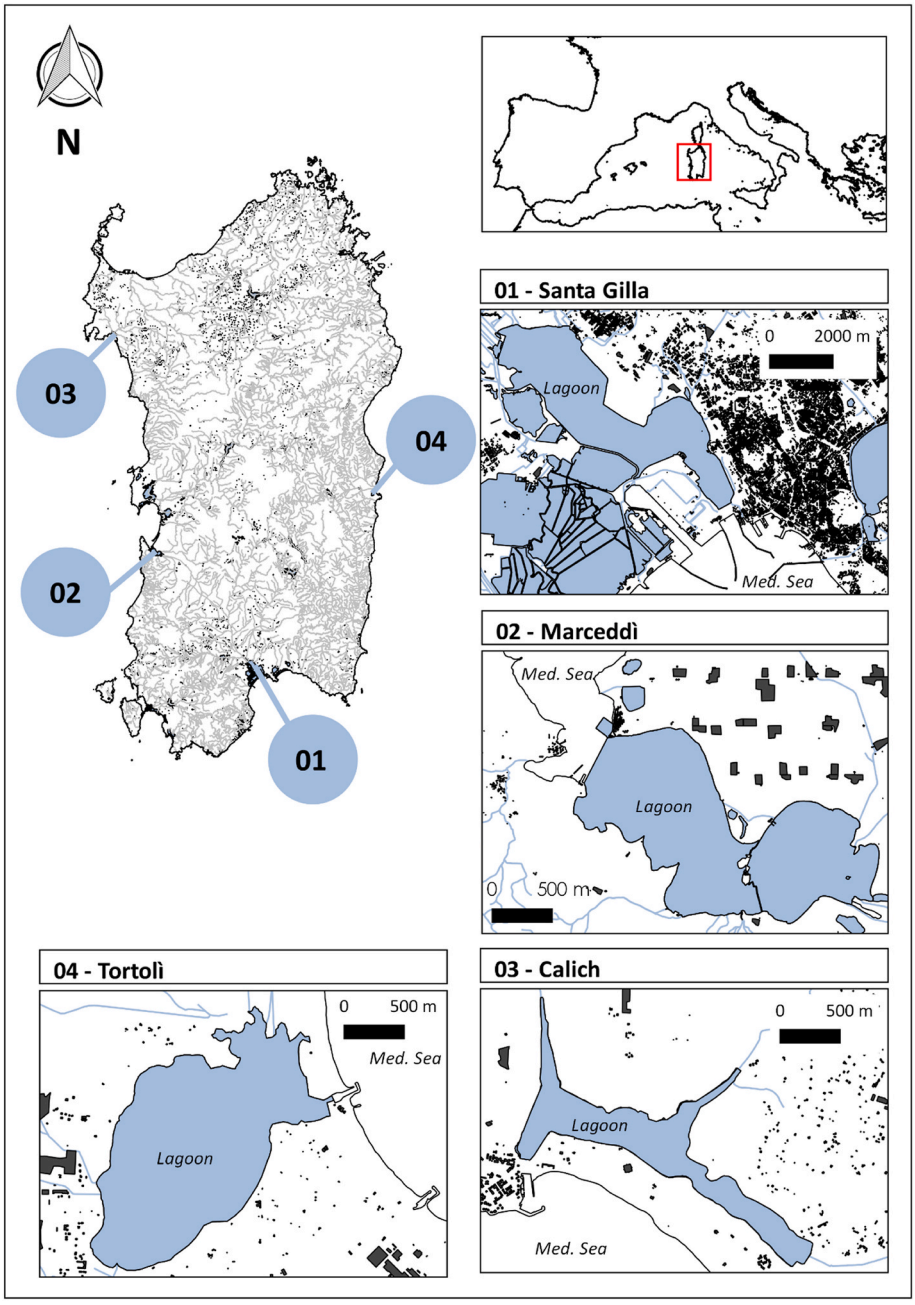

Fig. 1. Study area showing the location of the four Sardinian coastal lagoons analyzed.

aquaculture activities (Salati et al., 1999).

2.2. Sampling and environmental data

In June 2024, adult specimens of the European clam *R. decussatus*, of similar size were collected from natural shellfish banks in the lagoon of Santa Gilla. The clams were transported to the experimental Gillalab facility of the University of Cagliari (https://gillalab.it/), located near the Santa Gilla lagoon, and acclimated for 48 h before the start of the experiments at *in situ* temperature and salinity conditions at the time of sampling (21 °C and 38 PSU, respectively).

Temperature datasets for each lagoon were obtained from the Regional Environmental Protection Agency of Sardinia (ARPAS), as part of the monitoring carried out under the Water Framework Directive (2000/60/CE) obligations. Due to the coarse temporal and spatial resolution of the data, the dataset was aggregated to calculate temperature seasonal means (Winter, Spring, Summer and Fall) for the reference period 2017-2022. Additionally, the projection of future temperature was obtained from the air temperature projections at 2050 proposed by the Centro Mediterraneo per i Cambiamenti Climatici (CMCC; https://www.cmcc.it/it/scenari-climaticiper-litalia), based on IPCC Representative Concentration Pathways (RCP) 4.5 and 8.5. RCPs likely represent future temperature predictions under different global greenhouse gas and aerosol emissions: RCP 4.5 scenario (1.5 °C increase) reflects moderate emissions, while RCP 8.5 (1.75 °C increase) predicts more extreme climate change impact (IPCC, 2023). Projected mean air temperature increases for Sardinia corresponded to approximately +1.5 °C under RCP 4.5 and + 1.75 °C under RCP 8.5. These projected air temperature increments were applied to the lagoon water temperature distributions, assuming a strong coupling between atmospheric and water temperature in shallow coastal systems, where limited depth and rapid air-water heat exchange promote rapid thermal responses

(Ferrarin et al., 2024).

Using the 'terra' R package (Hijmans, 2025), temperature rasters (50 m resolution) were generated for each lagoon, for the reference period and the two warming scenarios by applying inverse distance-weighted deterministic interpolation (IDW) (Isaaks and Srivastava, 1991).

2.3. Clams' respiration rate

The thermal tolerance of *R. decussatus* individuals (n = 192; shell length: 32.98 ± 4.25 mm; total weight: 6.58 ± 2.77 g) was investigated measuring their respiration rate (RR, $mgO_2\ h^{-1}\ g^{-1}$ DW), as a proxy of metabolic performances (Angilletta et al., 2010; Sokolova et al., 2012). RR were measured at 16 temperatures, ranging from 8 °C to 38 °C at 2 °C intervals (Fig. 2). The lowest temperature of 8 °C was fixed to represent the lagoon's lowest temperature, while the highest 38 °C value corresponded to unprecedented extremely warm conditions in the lagoon.

Before the experiment, the specimens' morphological conditions were checked to ensure their good status: integer organisms, no damaged valve and prompt ability in closing the valves. Specimens were randomly divided into 16 groups (n = 12 each) randomly assigned to the different experimental temperatures. The thermal performance experiments started exposing specimens to the water temperature measured at the sampling date (21 °C), which was then increased or decreased by 1 °C per hour until the experimental temperature was reached (Giomi and Pörtner, 2013; Prusina et al., 2014; Bosch-Belmar et al., 2022b; Marchessaux et al., 2022). Individuals were acclimatized for 24 h after reaching the experimental temperature. After the acclimatization organisms were individually placed in a respirometric chamber (volume: 600 mL) containing air saturated filtered water (Whatman GF/C, 0.45 μm). To ensure the constant mixing of the water, each chamber was stirred with a magnet bar and an individual stirring device (Widdows and Staff, 2006). No sediment was included in the respirometric chambers in order to standardize experimental conditions, avoiding potential confounding effects associated with sediment-water interactions, burrowing behaviour, and the presence of other organisms (e.g., microfauna and algae).

The respirometric chambers (4 controls without clams and 12 experimental chambers with one clam each) were distributed in four temperature-controlled circulated stable water tanks. A controlled chiller system and a thermostatic heater (Grant Optima TX150) were used to cool or heat the water and maintain experimental temperatures. The dissolved oxygen concentration and temperature were measured simultaneously with 4 optical oxygen meters (Pyro Science® Firesting O2) each equipped with four optodes (16 optodes in total) and one sensor for temperature (Fig. 2).

Oxygen concentration was measured every second for at least 1 h, and at the end of the experiment, respiration rate was calculated according to the following equation (Sarà et al., 2013):

$$RR = (C_{t0} - C_{t1}) \times Vol_r \times 60 \times (t_1 - t_0)^{-1}$$

where: Ct_0 was the oxygen concentration at the beginning of the measurement, Ct_1 was the oxygen concentration at the end of the measurement, Vol_r was the volume of water in the respirometric chamber, 60 refers to the measurement time (in seconds) and, t_0 and t_1 correspond to the starting and end times of the experiment. At the end of the experiment, the mollusc flesh from each specimen was separated from the shell, dried at 110 °C for 24 h, and then weighed to determine the dry weight (DW, g). The RR was then normalized per hour and divided by the dry mass to obtain the individual oxygen consumption, expressed in $mgO_2\ h^{-1}\ g^{-1}$ DW. The net individual RR was then obtained by subtracting the oxygen consumption measured in control (CTRL) chambers (Marchessaux et al., 2022).

2.4. Thermal performance curves

Temperature was treated as a continuous variable, and the analysis focused on modelling the relationship between temperature and metabolic performance (RR), rather than testing for differences among temperature treatments. This approach is consistent with standard methods used in thermal performance curve analyses (Angilletta et al., 2010; Sokolova et al., 2012).

The thermal performance curves (TPCs) analysis was performed using the R package rTPC, which compares 24 non-linear least-squares models (Padfield et al., 2021). The model delong_2007 was excluded from the analysis because it failed to converge and adequately fit the data (Table S1). The model with the lowest Akaike Information Criterion score corrected for small sample size (AICc) was selected as the best fit (Padfield et al., 2021; Bosch-Belmar et al., 2022b; Marchessaux et al., 2024). Subsequently, a bootstrapping procedure was performed to calculate 95% prediction limits for the best TPC model and estimate confidence intervals around its temperature optimum. Respiration rates measured at 32-34 °C were excluded because they reflect transient stress responses (e.g. intermittent valve closure) rather than sustained metabolic performance, whereas data at 36-38 °C were retained to constrain the upper critical thermal limit (CTmax) of the species (Sokolova et al.,

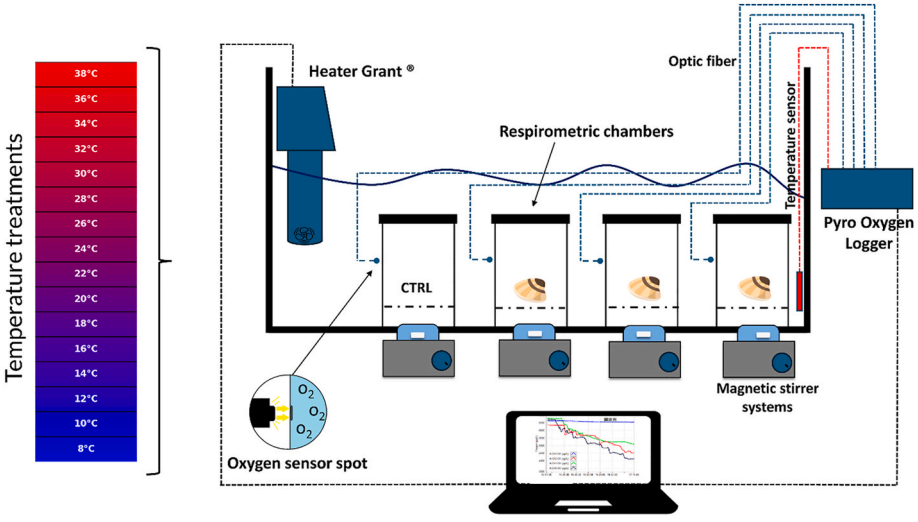

Fig. 2. Simplified design of the mesocosm setup to assess respiration rates of *R. decussatus* across 16 temperature values. Each set of the illustrated four respirometric chambers was replicated four times (for a total of 12 individuals per temperature).

2012; Prusina et al., 2014; Bosch-Belmar et al., 2022b; Marchessaux et al., 2022). Parameters related to the maximum respiration rate (*rmax*), the optimal temperature (*Topt*) and the shape parameter (*a*) were extracted from the TPC model and used to construct the thermal habitat suitability maps.

2.5. Mapping the reference and future thermal habitat suitability

Before integrating the TPC to temperature raster layers, the respiration rate data were converted into Thermal Habitat Suitability (THS) probability (between 0 and 1) for each experimental temperature following the formula proposed by Bosch-Belmar et al. (2022b):

$$THS = \frac{RR_t}{RR_{opt}}$$

where THS represents the Thermal Habitat Suitability index calculated for each season, RR_t represents the respiration rate at temperature T and RR_{opt} the value of respiration rate at the optimal temperature predicted by the best fitting TPC model. THS values where then calculated at pixel level (50 m spatial resolution), for each season and for the reference and future scenarios, assuming a homogeneous distribution of the species in the lagoon. Additionally, to highlight spatial-seasonal differences in habitat suitability of *R. decussatus* in the Sardinian lagoons between the reference period (2017-2022) and the future climatic scenarios (2050 RCP 4.5 and RCP 8.5), subtractions between future and present raster files were calculated using the formula:

$$\%\ of\ change = \left(THS_{2050\ RCPs} - THS_{2017/2022}\right)$$

The obtained new raster layers allowed identifying increasing or decreasing spatial occurrence probability of the species at the pixel scale and produce maps of expected change.

Finally, to visualize for comparison purposes seasonal changes in THS probability in the four lagoons under scrutiny we determined the density of THS values for either the reference and the two future scenarios using the 'ggridges' R package. This approach was intended to provide a comparative visualization of THS distributions rather than to perform inferential statistical testing.

3. Results

3.1. Respiration rates and thermal performance curves

The respiration rate of *R. decussatus* increased from 0.07 ± 0.04 $mgO_2\ h^{-1}\ g^{-1}$ DW at 8 °C to 1.55 ± 0.40 $mgO_2\ h^{-1}\ g^{-1}$ DW at 26 °C, and then decreased sharply at higher temperatures 30 °C dropping to 0.54 ± 0.33 $mgO_2\ h^{-1}\ g^{-1}$ DW. Respiration rate became negligible at 38 °C coinciding with the mortality of all specimens.

The best-fitting model was the Deutsch regression (Deutsch et al., 2008), which showed the lowest AICc score among the candidate models (Table S1). Model parameters were statistically significant ($p < 0.05$), and the model exhibited low residual standard error (SE = 0.25) (Table 1).

The best-fitting TPC showed a left-skewed shape (−0.44), consistent with a relatively high tolerance to elevated temperatures. RR increases progressively with temperature, peaking at the thermal optimum (T_{opt} = 26.71 °C), then drops steeply (a = 5.17) toward the critical and deadly thermal maximum (CT_{max} = 38 °C) (Fig. 3a), highlighting a narrow margin between optimal and lethal conditions. The peak performance (r_{max}) of *R. decussatus* overlaps the optimal temperature (*Topt*) at which the species reached a respiration rate of 1.64 $mgO_2\ h^{-1}\ g^{-1}$ DW (Table 1).

The THS probability curve derived from TPC range from 0 to 1, corresponding to the red-green color gradient. Highest suitability values occurred between 22 and 31 °C, representing optimal thermal conditions (Fig. 3b). The two lower pejus ranges were identified between 19-22 °C and 31-34 °C, while the upper pejus occurred between 17 and 19 °C 34-36 °C. Pessimum conditions corresponded to 14-17 °C and 36-

Table 1
Equation and performance estimates of the best-fitting model parameters. r_{max} = maximum respiration rate; T_{Opt} = optimum temperature, CT_{max} = critical (lethal) maximum temperature; T = point temperature; a = shape/symmetry parameter of the curve; ESD = estimated standard deviation; t = t Student's values; P = probability value. *** = P < 0.001.

$$R(T) = r_{max} \times \left(\frac{T - T_{Opt}}{T_{Opt} - CT_{max}}\right)^{a} \times exp\left[a \times \left(1 - \frac{T - T_{Opt}}{T_{Opt} - CT_{max}}\right)\right]$$

Curve parameters	ESD	t	P
r_{max}	1.63	44.99	***
T_{opt}	26.71	47.45	***
CT_{max}	38.00	174.53	***
a	5.17	15.56	***
Residual standard error (SE): 0.25			

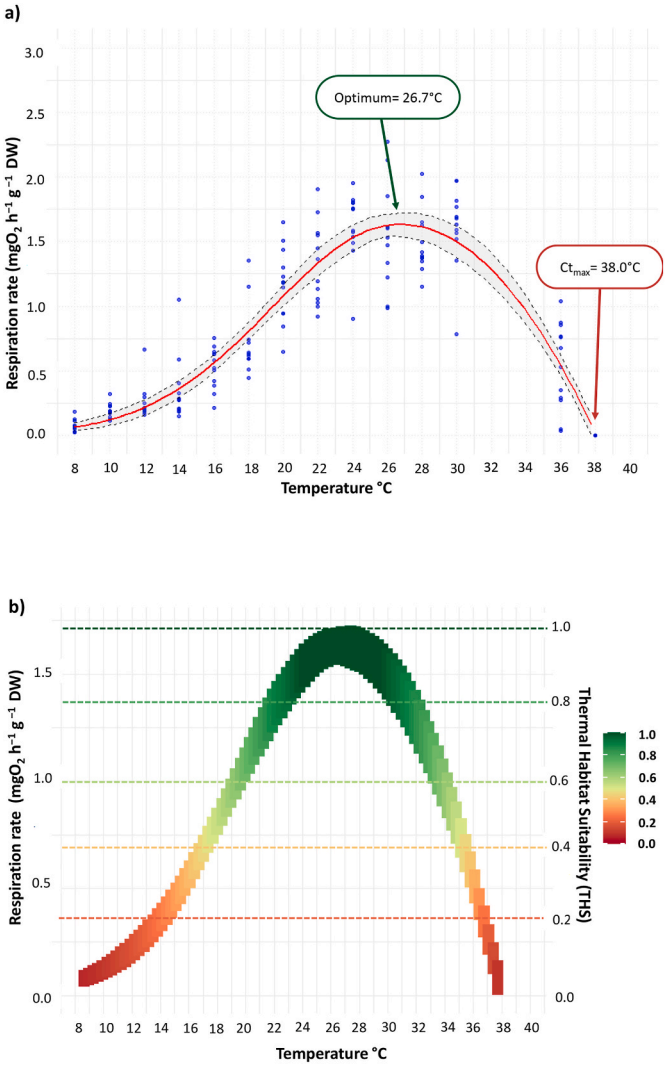

Fig. 3. Best-fitting Thermal Performance Curve (TPC, a) of *R. decussatus* based on the respiration rates ($mgO_2\ h^{-1}\ g^{-1}$ DW) and Thermal Habitat Suitability (THS, b) ranging from low (0) to high (1) species' thermal habitat suitability probability. Different colors in the THS curve represent ranges of *optimum* (0.8-1.0), *lower* and *upper pejus* (0.8-0.6 and 0.6-0.4), *pessimum* (0.4-0.2), and *lethal* (<0.2) temperature (Sokolova et al., 2012). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

37 °C, whereas lethal temperature ranges occurred at 8-14 °C and 37-38 °C.

3.2. Surface seasonal temperature

Seasonal thermal regimes varied distinctly across the four lagoons, each of which showed also specific spatial patterns (Figs. S1–S4; Table S2).

During the reference period (2017-2022), Santa Gilla showed the largest seasonal thermal variability, with winter temperatures averaging 11.47 ± 0.41 °C and summer means reaching 26.45 ± 0.32 °C (Fig. S1). Spring and fall displayed intermediate values (16.56 ± 0.67 °C and 18.04 ± 0.22 °C) respectively. Strong spatial gradients were evident, with the shallow inner sectors warmer than the marine-influenced inlet areas, especially in summer, when central and northern zones frequently exceeded 27-29 °C. Under future scenarios, temperatures increased across all seasons, reaching 12.97 °C (RCP 4.5) and 13.22 °C (RCP 8.5) in winter, and 27.95-28.20 °C in summer. These trends are projected to amplify existing gradients, with inner shallow zones likely to exceed 30 °C during summer, indicating increased exposure to thermal stress.

Marceddì lagoon displayed intermediate seasonal variability (Fig. S2), with winter means of 13.18 ± 0.27 °C, increasing to 17.76 ± 0.29 °C in spring, peaking at 28.14 ± 0.11 °C in summer, and decreasing to 19.52 ± 0.40 °C in fall. Temperature distribution followed a similar spatial pattern, with cooler waters near the marine connection and warmer conditions toward the inner sectors. Under RCP projections, winter temperatures increased to 14.7-14.9 °C, while summer means reached 29.6-29.9 °C, with shallow central areas approaching or exceeding 30 °C under RCP 8.5.

Calich lagoon, the smallest and most enclosed system, exhibited marked seasonal variability (Fig. S3). Mean winter temperatures averaged 14.78 ± 0.19 °C, increasing to 20.53 ± 0.65 °C in spring, reaching 26.61 ± 0.41 °C in summer, and declining to 19.28 ± 0.41 °C in fall. Spatial maps revealed heterogeneous temperature distribution, with warmer inner sectors and cooler areas near the sea inlet due to the water exchange. Under future scenarios winter temperatures increased to 16.28-16.53 °C, while summer means reached 28.11-28.36 °C.

Tortolì lagoon exhibited the most thermally stable regime among the four lagoons (Fig. S4). Mean temperatures ranged from 14.38 ± 0.29 °C in winter to 20.11 ± 0.28 °C in spring, peaked at 27.57 ± 0.23 °C in summer, and decreased to 21.23 ± 0.06 °C in fall. Future projections indicate moderate and uniform warming across seasons, with winter temperatures rising to 15.88-16.50 °C and summer temperatures reaching 29.07-29.32 °C under RCP scenarios. Spatial pattern showed warmer central sectors during spring and summer, while areas near the sea inlet remained cooler due to marine influence.

3.3. Seasonal variation in thermal habitat suitability probability

THS probability values showed remarkable seasonal variations at all lagoons under both reference and warming scenarios (Figs. 3–5, Fig. S5–S8).

Under the reference period summer represented the most favorable season for *R. decussatus* with THS values approaching optimal conditions (THS >0.98) across all lagoons (Fig. 4). Conversely, winter represented the least suitable season, with THS distribution concentrated within the pessimum range (THS <0.4). The lowest winter THS values were observed in Santa Gilla (0.11 ± 0.01) and Marceddì lagoons (0.17 ± 0.01), whereas Calich and Tortolì showed slightly higher, though unfavorable, conditions (0.26 ± 0.01 and 0.24 ± 0.01, respectively). In spring, THS values increased in all lagoons. Santa Gilla remained within the pessimum range (0.38 ± 0.04), whereas Tortolì and Marceddì reached upper pejus conditions (0.54 ± 0.02 and 0.47 ± 0.02, respectively). Calich lagoon exhibited the greatest improvement, reaching lower pejus conditions (THS = 0.70 ± 0.05). During fall, THS values were comparable to those observed in spring, although overall suitability remained high. Tortolì lagoon showed the most favorable fall thermal conditions, with a mean THS of 0.76 ± 0.004.

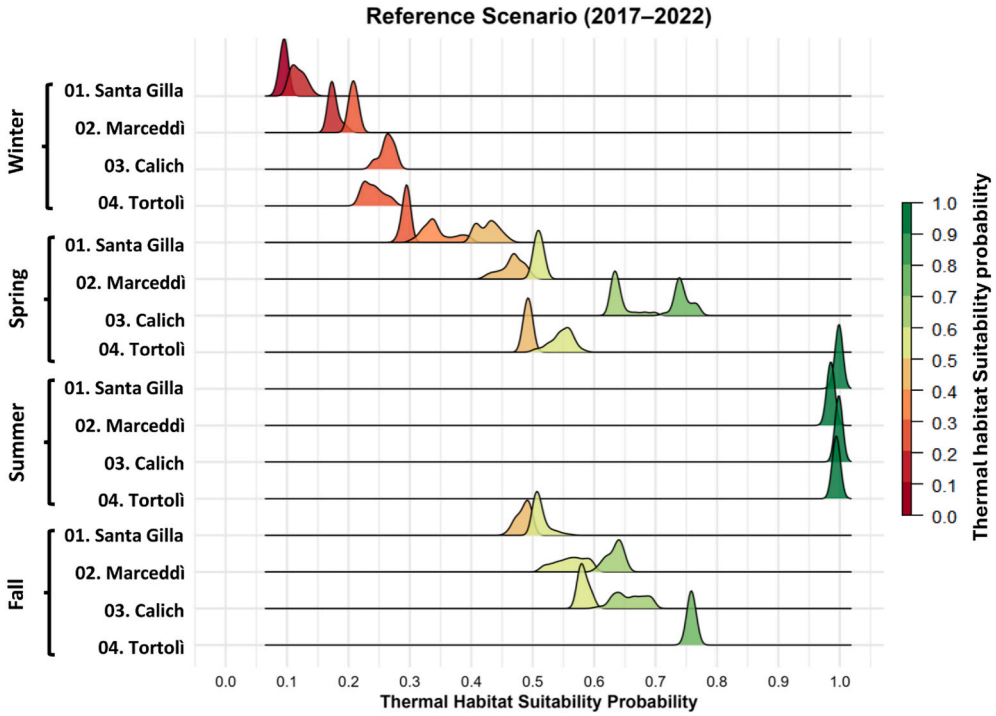

Fig. 4. Kernel density distributions of the predicted Thermal Habitat Suitability (THS) for *R. decussatus* under the reference scenario (2017–2022), shown for each season (winter, spring, summer, and fall) across the four investigated lagoons. Colors follow the THS probability gradient reported in Fig. 3b, ranging from unfavorable conditions (dark red, THS = 0) to favorable conditions (green, THS = 1). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

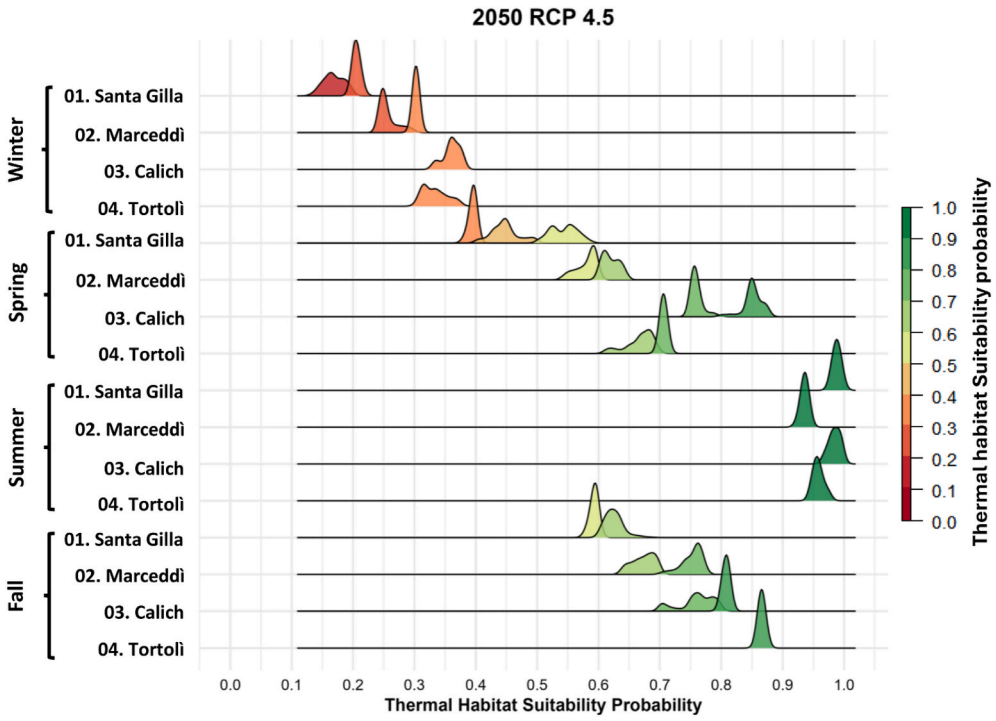

Fig. 5. Kernel density distributions of the predicted Thermal Habitat Suitability (THS) for *R. decussatus* under the 2050 RCP 4.5 warming scenario, shown for each season (winter, spring, summer, and fall) across the four investigated lagoons. Colors follow the THS probability gradient reported in Fig. 3b, ranging from unfavorable conditions (dark red, THS = 0) to favorable conditions (green, THS = 1). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Under the 2050 RCP 4.5 scenario, the THS showed a general improvement across all lagoons except during summer, when values slightly decreased (Fig. 5). The largest decline was recorded in Marceddì lagoon (−5.6%), followed by Tortolì (−3.6%), Calich (−1.4%) and Santa Gilla (−1.02%) (Fig. S9).

Under the 2050 RCP8.5 scenario, overall suitability increased

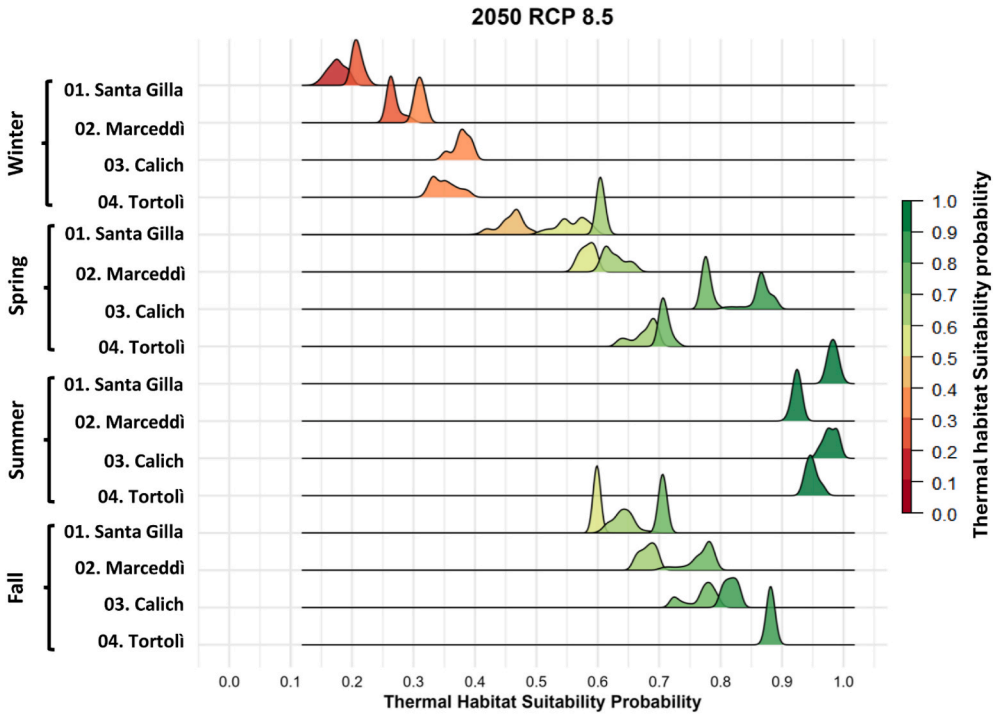

Fig. 6. Kernel density distributions of the predicted Thermal Habitat Suitability (THS) for *R. decussatus* under the 2050 RCP 8.5 warming scenario, shown for each season (winter, spring, summer, and fall) across the four investigated lagoons. Colors follow the THS probability gradient reported in Fig. 3b, ranging from unfavorable conditions (dark red, THS = 0) to favorable conditions (green, THS = 1). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

relative to the reference period, while seasonal contrasts remained pronounced (Fig. 6). Winter remains largely unfavorable (THS <0.4), while spring conditions approached near-optimal values. Summer suitability decreased slightly across all lagoons, while fall conditions remain favorable, indicating a temporal extension of thermally suitable habitats into late fall (>12%).

3.4. Spatial patterns of thermal habitat suitability probability

Spatial patterns of the THS differed among lagoons but generally showed inter-lagoon limited heterogeneity (Figs. S5–S8).

In Santa Gilla lagoon, during the reference period winter THS was uniformly low (Fig. S5). Under future scenarios, winter suitability increased, particularly in the central sectors, where THS values locally reached 0.23 under RCP 8.5, although conditions remained largely unfavorable (0.18 ± 0.01). In spring, spatial gradients emerged, with higher suitability in the innermost areas of the lagoon (THS = 0.47) and lower values toward the southeastern sector near the sea inlet (THS = 0.27). During summer, THS became homogeneous and optimal across the entire lagoon in both reference and warming scenarios. In fall, spatial heterogeneity reappeared, with higher values in the inner sectors (THS = 0.56) and lower suitability in the central areas (THS = 0.45). Under both RCP 4.5 and RCP 8.5 scenarios, spatial differences observed in spring and fall progressively weakened, resulting in a more homogeneous distribution of THS values.

In Marceddì lagoon, spatial variation was generally low, across all lagoons' sectors (Fig. S6). During winter and fall, higher suitability values were observed near the sea inlet THS = 0.22 and 0.66, respectively). A contrasting pattern emerged in spring, when the inner lagoon' sectors showed higher suitability (THS = 0.52). Under future warming scenarios, spatial contrasts progressively decreased, resulting in a more homogeneous THS across the lagoon.

In Calich lagoon, more pronounced spatial gradients in THS were observed compared to the other lagoons, particularly during spring and fall (Fig. S7). Lower THS values occurred in the sea-influenced sector (THS = 0.62), whereas higher suitability was recorded in the inner part of the lagoon (THS = 0.68). From summer onward, spatial contrasts decreased and became uniform. Under RCP scenarios, these gradients were further attenuated, indicating progressive homogenization of suitability patterns.

In Tortolì lagoon, spatial variability in THS was very limited throughout the year (Fig. S8). Only minor reductions in suitability were observed near the sea inlet during spring (THS = 0.49), whereas the rest of the lagoon maintained relatively homogeneous conditions. Under both RCP 4.5 and RCP 8.5 scenarios, spatial patterns remained unchanged, indication stable widespread THS across the lagoon.

4. Discussion

This study provides the first assessment of thermal performance for the European clam *Ruditapes decussatus*, one of the most ecologically and commercially relevant benthic species inhabiting Sardinian coastal lagoons. By combining controlled respirometric experiments with nonlinear modelling of thermal performance curves (TPCs), we identified key physiological thresholds and characterized the species' sensitivity to temperature. These experimentally derived parameters were then used to model the thermal habitat suitability (THS) of *R. decussatus* across four Sardinian lagoons under a reference period (2017-2022) and two future climate scenarios (RCP 4.5 and RCP 8.5).

Our results show that respiration rate varies greatly across the tested temperature range (8-38 °C), revealing a wide thermal tolerance window. The highest respiration rate (r_{max} 1.64 $mgO_2\ h^{-1}\ g^{-1}$ DW) was recorded at the optimal temperature (T_{opt}) of 26.71 °C. These findings are only partially consistent with previous studies, which reported temperatures above 27 °C as already stressful (Sobral and Widdows, 1997) and identified a thermal window of 10-30 °C with the maximum respiration around 25 °C (Bodoy et al., 1986). This discrepancy between our results and previous studies likely arises from at least two factors. First, our study and the previous ones are based on different experimental approaches, with the latter being based on *R. decussatus* thermal tolerance rather than on estimates of the thermal performance physiology. Secondly, it has been recently shown that, as for any other aquatic invertebrates, populations from different geographical areas exhibit different thermal physiology and performance curves, due to genetically modulated physiological traits in different thermal assets (Bing-Xian et al., 2025). In Sardinian lagoons *R. decussatus* experienced summer temperatures exceeding 33 °C, which may contribute to local thermal adaptation (Magni et al., 2008; Foti et al., 2014; Cataudella et al., 2015; Batanero et al., 2022). Moreover, respiration rate in bivalves is influenced by thermal history, activity level, body size, and reproductive status (Han et al., 2008).

The TPC curve exhibited a left-skewed shape (−0.44), suggesting relatively high tolerance to elevated temperatures (Angilletta et al., 2010). Nevertheless, all specimens exposed to 38 °C died within 24 h, defining the critical thermal maximum (CT_{max}). This transition from optimal to lethal conditions (*sensu* Sokolova et al., 2012) likely reflects heat-induced molecular stress responses and increasing energetic costs (Giomi and Pörtner, 2013). Mortality was preceded by behavioral responses such as valve gaping and inactivity consistent with “heat coma” conditions described in other bivalves (Ansell et al., 1981). Despite this threshold, the CT_{max} values fall within the range reported for other marine invertebrates inhabiting thermally variable environments. For example, the flat oyster *Ostrea edulis* shows optimal performance near 26 °C and functional decline above 32-34 °C (Götze et al., 2025), while the tropical oyster *Pinctada margaritifera* tolerates up to about 34 °C (Lugue et al., 2025). These findings suggest convergent physiological responses to thermal stress across marine bivalves (Madeira et al., 2012).

As benthic burrowing organisms, bivalves of the genus *Ruditapes* exhibit behavioral adaptations to cope with environmental stressors, including temperature fluctuations (Helmuth et al., 2002). Among the behavioral strategies adopted by bivalves in response to acute thermal stress, valve closure is the most common one (Domínguez et al., 2020, 2023). By reducing the exposure to water stressors, bivalves reduce their metabolic activity and conserve energy (Ortmann and Grieshaber, 2003). However, this mechanism may be less effective in infaunal species, like *R. decussatus*, which usually have shell made of aragonitic material (Iglikowska et al., 2023), which conducts heat efficiently to tissues (Gómez-Martínez et al., 2002). Other adaptative behaviors include increasing borrowing depth and duration (Bertolini and Pastres, 2021; Domínguez et al., 2021). In this regard, we noticed that *R. decussatus* can burrow down to 8 cm (Macho et al., 2016). According to these results, we must acknowledge that our experiment was carried out in extremely simplified conditions (e.g., without sediments), so that the very high resistance to high temperatures reported here could be partially a procedural effect. Nonetheless, it must be considered that burrowing bivalves like *R. decussatus* need to obtain O_2 from the water, so that, at a certain point neither the valve closure mechanism, nor a deeper burrowing position in the sediment will allow the clam to further tolerate the thermal stress.

The physiological response described above translates into significant spatial and temporal variability in THS across lagoons. Under the reference period, THS is lowest in winter and increases progressively through spring, reaching optima values in summer (THS probability >0.9 in all lagoons), before declining in fall as temperatures cooled. Across the four lagoons, THS maps reveal contrasting levels of spatial heterogeneity. Santa Gilla and Calich lagoons exhibit the strongest spatial gradients, particularly in winter and spring, reflecting pronounced inner-outer thermal contrasts. Marceddì shows moderate spatial patterns, with THS alternating between higher values near the sea inlet and in the inner lagoon. In contrast, Tortolì displays consistently low spatial heterogeneity, with largely homogeneous THS values

throughout the lagoon.

High summer THS values are consistent with the reproductive cycle of *R. decussatus*, which includes gonadal maturation in spring, spawning and recruitment in summer, and a resting phase in winter (Ojea et al., 2004; Matias et al., 2013). This confirms that thermal conditions play a key role in regulating reproductive processes in bivalves, as gonadal development, spawning, and larval development are strongly influenced by increasing water temperature (Delgado and Pérez Camacho, 2007; Chícharo and Chícharo, 2001a). The potential anticipation of *R. decussatus* reproductive period in early spring, driven by rising water temperatures, could positively prompt spawning. Nonetheless, the typical lower salinity values in spring of Mediterranean lagoons (Ghezzo et al., 2011), could significantly affect the recruitment success of *R. decussatus*. The timing and success of larval settlements in bivalves are, indeed, strongly influenced by the combination of different environmental variables, including the interaction between temperature and salinity (Borsa and Millet, 1992). Early reproduction, indeed, could expose larvae and juveniles to suboptimal conditions due to lower values of salinity. In particular, the combination of elevated water temperatures and reduced salinity has been linked to high mortality rates in both juveniles and adults, highlighting the species' sensitivity to multiple rather than single environmental stressors (Rato et al., 2022).

However, based on our approach and results, the potential ecological consequences of an earlier onset of the reproductive period of *R. decussatus* in early spring remain largely uncertain. Species distribution and abundance are influenced by multiple interacting factors, among which temperature and salinity are primary, but not exclusive, drivers (Chícharo and Chícharo, 2001b; La Peyre et al., 2013; Rato et al., 2022). Survival, growth, and reproductive performance of bivalve mollusks are in fact regulated also by the substrate typology and trophic resource availability (Gharbi et al., 2016; Abdelhady et al., 2019), which, in turn, can also be affected by water warming (Liu et al., 2024).

Future projections indicate an overall increase in THS across lagoons, particularly in winter and spring, while summer remains optimal and fall becomes more suitable. At the same time, spatial variability is expected to decrease, leading to homogenization of thermal conditions. Such loss of environmental heterogeneity may have broader ecological consequences, as physical homogenization can alter biogeochemical processes and community structure (Lejeusne et al., 2010; Mora et al., 2013).

Given the central role of temperature in regulating bivalve physiology, a THS modelling approach provides a useful framework for anticipating climate-driven changes in lagoon ecosystems. Our findings suggest that warming may shift the timing and duration of favorable thermal windows for *R. decussatus*, with potential implications for population dynamics. Although additional drivers (e.g. salinity, sediment characteristics and ecological interactions) were not included, integrating THS results into management strategies could support adaptative aquaculture and conservation planning. In particular, THS-based approaches may help optimize harvesting calendars, reduce exposure to thermal stress, and enhance the resilience of traditional lagoon fisheries. While future studies should incorporate multiple environmental factors, temperature-based modelling represents a robust first step toward climate-informed management.

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CRediT authorship contribution statement

Francesco Palmas: Conceptualization, Data curation, Formal analysis, Writing – original draft, Writing – review & editing. **Arianna Gentili:** Data curation, Formal analysis, Writing – review & editing. **Serenella Cabiddu:** Writing – review & editing. **Viviana Pasquini:** Writing – review & editing. **Pierantonio Addis:** Writing – review & editing. **Gianluca Sarà:** Writing – review & editing. **Mar Bosch-Belmar:** Writing – review & editing. **Mario Francesco Tantillo:** Writing – review & editing. **Antonio Pusceddu:** Conceptualization, Funding acquisition, Supervision, Writing – original draft, Writing – review & editing.

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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2026.108139.

Data availability

Data will be made available on request.

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