Received: 2 March 2024 | Accepted: 8 July 2024

DOI: 10.1111/1365-2435.14620

Functional Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Predicting key ectotherm population mortality in response to dynamic marine heatwaves: A Bayesian-enhanced thermal tolerance landscape approach

Jahangir Vajedsamiei[1] | Niklas Warlo[1] | H. E. Markus Meier[2] | Frank Melzner[1,3]

[1]Department of Marine Ecology, GEOMAR Helmholtz Centre for Ocean Research Kiel, Kiel, Germany

[2]Department of Physical Oceanography and Instrumentation, Leibniz Institute for Baltic Sea Research Warnemuende (IOW), Rostock, Germany

[3]Christian-Albrechts-Universität Kiel, Kiel, Germany

Correspondence
Jahangir Vajedsamiei
Email: jvajedsamiei@geomar.de and jahangir.vajedsamiei@gmail.com

Funding information
European Commission EU H2020-INFRAIA, project AQUACOSM-plus, Grant/Award Number: 871081

Handling Editor: Diego Barneche

[Correction added on 23 July 2024, after first online publication: Affiliation 3 has been removed for H. E. Markus Meier and affiliation 4 has been renumbered to 3.]

Abstract

1. As climate change intensifies heatwaves, quantifying associated mortality within ectothermic populations is crucial for effective conservation. Thermal tolerance landscape (TTL) models are useful predictive tools that assume exponentially decreasing survival durations in individuals with increasing temperatures. This assumption has been validated through regression analyses on data from constant temperature experiments, primarily focusing on adult-stage individuals. However, this approach does not allow for direct model validation with data from dynamic, real-world heatwave events and overlooks early recruitment stage vulnerabilities.
2. This study aimed to address these gaps using the blue mussel *Mytilus*, a foundation species forming extensive reefs along temperate coasts, as a model organism. We monitored survival rates of mussels (juveniles and adults) under constant heatwave (CHW) conditions in a laboratory experiment and under dynamic heatwave (DHW) scenarios simulated in an outdoor mesocosm experiment. Post-heatwaves, we also assessed recruitment rates within the mesocosms. TTL models were parametrised by employing Approximate Bayesian Computation with Sequential Monte Carlo (ABC-SMC) on each dataset separately.
3. The parameter distributions were similar across both experiments, and the ABC-SMC model predictions closely matched the observed survival declines, validating these models. In comparison, we found a lower predictive performance when using a Bayesian regression approach. Additionally, our best-fit model predicted that warming across the non-fatal DHW regimes would increase sublethal effects on mussels. The observed impact on the recruitment stage was more pronounced, with the recruitment rate following an exponential decay as sublethal effects increased. Our model projected minor (<4%) sublethal effects in adult mussels during the century's five warmest summer temperature regimes, corresponding to 0%–32% declines in recruitment rates.
4. Our research extends the TTL model validation, demonstrates the resilience of subtidal Baltic *Mytilus* to future extreme heatwaves and offers an approach to

predict heatwave-induced population mortalities, applicable to other species and sensitive systems.

KEYWORDS
ABC-SMC, Bayesian regression, heat stress, mesocosm, mussel life stages, ocean warming, selection pressure, sublethal effects

1 | INTRODUCTION

Anthropogenic global warming increases the frequency and intensity of heatwaves (IPCC, 2021; Laufkötter et al., 2020). These prolonged episodes of high temperatures are particularly hazardous during summer, posing significant risks to ectothermic species in sensitive habitats such as shallow marine environments (Garrabou et al., 2009; Hobday et al., 2016; Holbrook et al., 2019; Pinsky et al., 2019). These species, whose physiological functions are closely tied to ambient temperatures, show exponential increases in metabolic demands with rising temperatures (Pörtner et al., 2010). When temperatures exceed a critical threshold, a cascade of physiological disruptions ensue, affecting mechanisms from oxygen balance and cellular redox states to enzyme activities and membrane stability (Boutilier & St-Pierre, 2000; Ern et al., 2023; Pörtner, 2012; Sokolova, 2023; Somero, 2010). These stressful conditions can disproportionately impact sensitive life stages like larvae, which are crucial for the continuity of populations (Collin et al., 2021). High mortality rates among foundational taxa like corals, seagrasses and mussels can alter community structures, leading to profound ecological impacts (Bellard et al., 2012; Hughes et al., 2017; Seuront et al., 2019; Strydom et al., 2020; Wernberg et al., 2016). Concurrently, marine heatwaves exert a selective pressure that may favour thermally resilient individuals within populations, potentially driving evolutionary adaptations (Gilbert & Miles, 2017; Gomulkiewicz & Holt, 1995; Vajedsamiei, Wahl, Schmidt, Yazdanpanahan, & Pansch, 2021).

Quantifying population mortality rates during heatwaves is essential for developing early warning systems and guiding ecosystem conservation and aquaculture management in the face of climate change (Harley et al., 2006; Pecl et al., 2017; Poloczanska et al., 2013; Skirving et al., 2019). Thermal tolerance landscape (TTL) models, as termed by Rezende et al. (2014), have emerged as effective predictive tools, particularly at local scales. These models assume that as temperatures rise beyond a critical threshold, individuals' survival durations decrease exponentially. While the survival durations at a given temperature (intercepts) vary among individuals, the relative rate of decrease in their survival durations (sensitivity exponent) is the same across the entire population. This assumption has been rigorously tested through frequentist linear regression analyses on data from constant temperature experiments, focusing mainly on adult-stage individuals (Bigelow, 1921; Fry et al., 1946; Jacobs, 1919; Jørgensen et al., 2019, 2021; Rezende et al., 2020). As detailed mathematically in the Methods section (also see Fry et al., 1946; Jørgensen et al., 2019, 2021; Rezende et al., 2020), the TTL model can also be defined based on the *lethality build-up rate*—the rate at which organisms accumulate potentially lethal effects (Text S1). This rate is assumed to remain constant over time at a given temperature and is measured as the percent reciprocal of the survival duration (100/duration). A similar regression approach can then be used to derive the TTL model's key parameters, including the lethality build-up rate at a reference temperature (intercept) and the thermal sensitivity parameter (slope). Once parametrised, the TTL model can predict population survival rates by calculating the lethality build-up trajectories of individuals during dynamic heatwave events (Fry et al., 1946). However, controlled laboratory experiments, which often include pre-experimental acclimation and acute exposure to extreme temperatures, may not fully represent natural settings. In the wild, an organism's acclimation history—including variations in feeding conditions, gradually increasing temperatures, or early heat spikes—can influence resilience to severe temperatures during heatwaves (Georgoulis et al., 2022; Helmuth et al., 2004). Despite these concerns, several studies have found that regression-based TTL models provide reasonably accurate predictions for survival under dynamic temperature scenarios (Bertolini & Pastres, 2021; Fry et al., 1946; Jørgensen et al., 2021; Li et al., 2023; Rezende et al., 2020).

Still, there is a need to directly parametrise and validate TTL models using data from real-world dynamic heatwave events to establish the most probable parameter sets and predictions. Additionally, comparing TTL model predictions for older individuals with the vulnerability of early life stages remains uncertain.

This study aimed to address these gaps using the *Mytilus* mussel, a foundation species that forms extensive reefs in the Western Baltic Sea and other temperate coasts, as a model organism. We monitored the survival rates of mussels (juveniles and adults) under two distinct conditions: one in a controlled laboratory setting with constant heatwave (CHW) conditions and another in outdoor mesocosms that simulate natural, dynamic heatwave (DHW) scenarios. Post-heatwaves, we also conducted recruitment counts within the mesocosms. We employed approximate Bayesian computation with sequential Monte Carlo (ABC-SMC) on each dataset to parametrise the TTL model. We compared the posterior distributions between experiments and contrasted predicted survival trajectories directly with the observed survival rates to validate the model assumptions and assess their versatility across different heatwave regimes. We also evaluated the predictive power of the ABC-SMC approach against a Bayesian regression approach. Additionally, we examined the severity of DHW regimes' impacts on recruitment rates compared to older-stage mussels. Finally, we applied the best TTL model and the empirical insights to project the mussel population's responses to the five warmest summer regimes of the century, considering high CO_2 emission scenario temperature projections and daily temperature fluctuations.

2 | METHODS

2.1 | The study system

We utilised the blue mussel from the *Mytilus edulis* complex in the Western Baltic Sea as our model organism due to its extensive reef formations and significant ecological and economic roles (Burge et al., 2016; Larsson et al., 2017; Zippay & Helmuth, 2012). The Baltic Sea, experiencing rapid warming trends, provided a suitable setting for our predictive heatwave response modelling, supported by available future temperature projections (Meier et al., 2021; Reusch et al., 2018).

2.2 | Constant heatwave (CHW) experiment

The CHW experiment evaluated mussel survival under constant heatwave conditions. Mussels were exposed to temperatures of 26, 27, 28 or 29°C, levels known to cause mortality within days to weeks (Vajedsamiei, Wahl, Schmidt, Yazdanpanahan, & Pansch, 2021; Zittier et al., 2015).

On 6 July 2022, 320 mussels from two size classes (approximately 7 and 20 mm)—representative of different life stages (juveniles versus adults)—were collected from a location near GEOMAR at less than 0.2 m depth (54°19′45.4″ N 10°08′56.2″ E). They were acclimated for a week in 8-L aquaria at 17°C and fed daily with *Rhodomonas salina* (initial concentration of 1875 cells mL^{-1}) cultured at GEOMAR's Kiel Marine Organism Culture Centre, with water changes to mitigate ammonia.

From 12 to 15 July 2022, we set up eight thermal baths using the Kiel Indoor Benthocosm (KIB) system, featuring computer-controlled 600-L tanks (Pansch & Hiebenthal, 2019). In each, four 18-L cylinders held 1 μm filtered seawater: two as reserves (also housing a temperature probe) and two containing 2-L PVC baskets (5-mm mesh) placing mussels. On 15 July 2022, within a 10-min window starting at 12:00 am, 320 mussels were evenly distributed across 16 PVC baskets (80 per temperature, 40 per bath). Temperature was recorded hourly by the GHL system (Profilux 3.1TeX; GHL Advanced Technology) and verified daily with a handheld sensor (WTW Multi 3630 IDS), which also measured water salinity, pH and oxygen on July 15 and weekly after that. PVC baskets with mussels were transferred to the reserve cylinders containing seawater every 5 days, and water in used cylinders was replaced.

Mortality was assessed daily at noon, using unresponsiveness (no valve gaping) under mechanical stress. Dead mussels were stored in plastic bags until the experiment concluded on August 25, when their shell lengths were measured. Additional details on the setup and measurements can be found in Figures S1 and S2.

2.3 | Dynamic heatwave (DHW) experiment

The DHW experiment evaluated mussel survival and recruitment under near-natural, dynamic heatwave conditions. Four hundred and eighty mussels collected on 1 July 2022, were maintained in two 17°C aquaria for a week, following the same protocol as the CHW experiment. On 6 July 2022, these mussels were equally distributed across 12 PVC cages, each containing a mix of 20 small and 20 large-sized mussels. These cages were then installed in the 12 1400-L tanks of the Kiel Outdoor Benthocosm system (KOBs; detailed in Wahl et al., 2015), which additionally harboured regional shallow-water communities including macro-algae *Fucus*, seagrass *Zostera* and their associated species (Figure S1).

Three peristaltic pumps distribute non-filtered seawater (10,000 L day^{-1}) from the fjord to sets of four tanks. The computer-controlled units mimic near-natural temperature dynamics in the tanks where water is thoroughly mixed due to built-in circulation and a wave generator. Tanks in the experiment had dynamic temperature baselines, staggered from 0°C to 5.5°C at 0.5°C intervals (Figure S1). From 7 to 13 July 2022, temperatures in 11 tanks were adjusted to establish these baselines. We simulated DHWs from 29 July 2022 to 1 September 2022 by reducing inflow to 4000 L day^{-1} and increasing baseline temperatures by 2.5°C for all treatment levels. Adjustments occurred between 9:00 and 10:00 am, with the baseline returning to ambient Kiel Fjord temperatures on 1 September 2022. Temperature was recorded hourly, O_2, pH and salinity were recorded daily, and chlorophyll levels were measured weekly, as detailed in Figures S3–S5.

By the end of the DHW experiment (8 September 2022), mussel survival and sizes were assessed using the methods described for the CHW experiment. To evaluate mussel recruitment, four settlement panels were installed on 2 June 2022 in all 12 tanks near but not in direct disposal of the wave generator and above the *Fucus* habitats so that larval mussels could attach, metamorphose and grow in the absence of predators. The panels consisted of two types, each with two variants: PVC panels in sizes 0.3 × 6 × 6 cm and 0.5 × 6 × 6 cm and brick panels in sizes 3 × 3 × 3 cm and 3 × 6 × 6 cm. Recruitment data were collected at the end of the experiment, with settled mussels (1–10 mm final shell length) collected and counted. Our experiments did not require any ethical approval licence.

2.4 | Principles of thermal tolerance landscape (TTL) model

The principles of the TTL model are outlined in the following equations, which define how population survival rates change over time and temperature.

2.4.1 | Survival probability equations

$$P(t) = 1 - \frac{M_p(t)}{n_p}, \tag{1}$$

$$M_p(t) = \sum_0^t M_i, \tag{2}$$

$$M_i = \{\, 1, \text{if } L_i = 100; 0, \text{otherwise} \}. \tag{3}$$

Here, $P(t)$ represents the population's survival probability at time t. M_p indicates the total mortality within the population up to time t, and n_p is the population size. Individual mortality, denoted by M_i, is set to 1 when the accumulated lethality, L_i, reaches 100.

2.4.2 | Lethality build-up equations

$$L_i(t) = L_{i0} + \int_0^t \dot{L}_i(t)dt. \tag{4}$$

In this equation, $L_i(t)$ signifies the cumulative lethal heat stress that an organism experienced (*lethality build-up*) for an individual at time t, with $\dot{L}_i(t)$ denoting the rate at which lethality builds up at that specific moment. It can also be assumed there is no initial lethality build-up present prior to the heatwave exposure, $L_{i0} = 0$.

2.4.3 | Rate of lethality build-up equations

$$\dot{L}_i = \frac{100}{t_i}, \tag{5}$$

$$\dot{L}_i(t) = \dot{L}_{ir} \times 10^{k_p(T(t) - T_r)}. \tag{6}$$

Equation (5) calculates an individual's lethality build-up rate based on its survival time at a given temperature. As an individual's survival time decreases, the lethality build-up rate increases. Equation (6) adjusts the lethality build-up rate based on the difference between a reference temperature (T_r; an arbitrarily chosen lethal temperature) and the actual temperature over time $T(t)$ and the parameter k_p indicating the shared population-level sensitivity to temperature changes.

2.5 | Model parametrisation and validation

Survival patterns did not significantly vary between juvenile and adult mussels (sizes ca. 7 vs. 20 mm) in either the CHW or DHW experiment (Figure S6; Table S1). Consequently, the datasets from the two size classes were merged for further analysis.

We employed an approximate Bayesian computation with sequential Monte Carlo (ABC-SMC; Del Moral et al., 2012; Sisson et al., 2007) approach to parametrise the TTL model directly based on the data set from each experiment. The ABC could circumvent a direct calculation of the likelihood of observing DHW data given certain model parameters (Rubin, 1984) by simulating and contrasting data with observations to find the approximate posterior parameter distributions. The SMC technique enhanced the ABC by progressively refining parameter estimates through a series of weighted simulations, improving the posterior distributions' accuracy and efficiency (Text S2). The three TTL parameters were the temperature sensitivity parameter and the mean and standard deviation of the lethality build-up rate at a reference temperature, that is respectively denoted as k, mean$(\dot{L}_r)$ and SD$(\dot{L}_r)$, $\dot{L}_r$ on the decadic logarithm scale. The reference temperature was set at 28°C, known to cause mussel mortality. This reference temperature should not be confused with the threshold for lethality accumulation, which is undefined due to the model's exponential nature. The choice of reference temperature is trivial because the TTL model focuses on relative temperature changes, ensuring that its predictions remain accurate regardless of the specific reference temperature chosen.

Figure 1 illustrates a schematic overview of our ABC-SMC approach, conducted separately using the datasets from CHW and DHW experiments. The initial step involved sampling 5000 particles, each representing a potential set of the three model parameters, from Gaussian prior distributions. In the initial iteration of our algorithm, we input each prior particle (as a *proposal*) and temperature time series data into the TTL model to simulate four population survival trajectories for CHW or DHW scenarios. A proposal was retained if its mean absolute deviation (MAD) from the observed survival data across all four CHW or DHW samples remained below the pre-set initial MAD threshold (epsilon). The qualifying proposals were given equal probabilities to be resampled as new particles in the second iteration. In the second and later iterations, each new particle was perturbed by adding Gaussian noise to the parameter values and used as a proposal to produce data. Any particle that failed to produce valid data after 10 perturbation attempts was discarded. Using a Gaussian kernel, we recalculated the weights for each qualifying proposal in each iteration based on its proximity to the particle set from the previous iteration. The particle set was iteratively refined by systematically narrowing the acceptance MAD threshold. The process concluded when the particle acceptance rate fell below 20%, yielding a particle set effectively approximating the posterior distribution. This set offers insights into the most probable parameter values given the observed data. For a more extensive algorithm description, refer to Text S3.

In addition to the ABC-SMC, a Bayesian regression (BR) approach was used to parameterise the TTL model using the CHW data (detailed in Text S4). The BR represented a generalised form of the frequentist regression traditionally used for TTL parameterisation. While traditional frequentist regression methods could only rely on complete datasets, both Bayesian approaches could incorporate censored survival data, capturing partial mortality during less potent heatwaves—a common characteristic of data derived from natural events.

Overall, we parametrised the TTL model three times through ABC-SMC on CHW data, ABC-SMC on DHW data, and BR on CHW

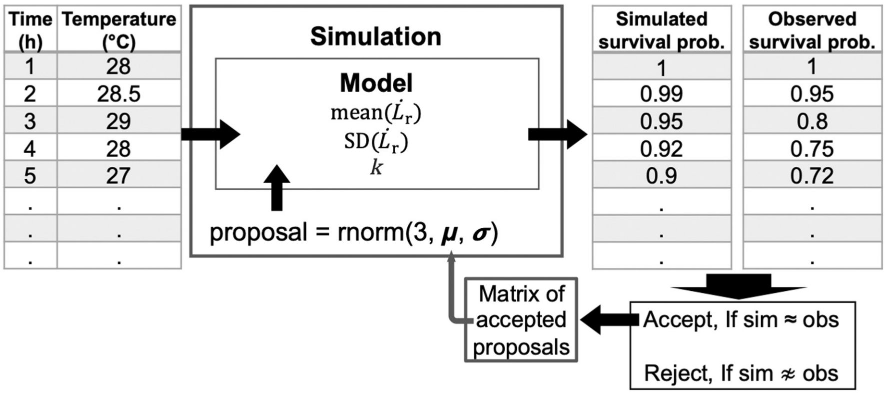

FIGURE 1 Schematic representation of the approximate Bayesian computation via sequential Monte Carlo (ABC-SMC) as used for refining parameters of the thermal tolerance landscape (TTL) model. The process began with inputting temperature time series data into the TTL model alongside randomly drawing parameter proposals from a normal prior distribution, indicative of prior beliefs about the parameters' likely values. The model iteratively simulated survival probabilities, compared to observed data using the mean absolute deviation (MAD) across all temperature series within an experiment for each proposal. Proposals yielding simulated probabilities with MAD within an acceptable range were retained, contributing to a matrix incrementally refined to form the posterior parameter distributions. Each iteration narrowed the acceptance threshold, integrating accepted parameters to calibrate subsequent simulations and enhance estimate precision. For an in-depth explanation of the methodology and the script, refer to Text S3. Displayed values are illustrative.

data. To validate and compare the models and compare the predictive performance between ABC-SMC and BR, the same data used for parametrisation were targeted for prediction. From the posterior parameters of each model, we sampled 1000 parameter sets based on their probabilities. For each set, the mean$(\dot{L}_r)$ and SD$(\dot{L}_r)$ were used as inputs to the *rlnorm()* function to simulate 100 random values of $\dot{L}_r$, for individual mussels, assuming a $\log_{10}$-normal distribution. Utilising these 100 $\dot{L}_r$ and the corresponding posterior sample of the population rate constant k, we predicted 400 individual lethality build-up (L_i) trajectories and four population survival trajectories for four heatwave regimes of the corresponding experiment. Finally, we calculated the MAD between the predicted and observed survival probabilities. The MAD statistics informed us about the precision of the posterior predictions. A low MAD value would indicate support for the model assumptions.

To assess the generalisability of the TTL assumptions, we compared the posterior distributions derived by ABC-SMC between the experiments. Additionally, we evaluated how well the models parametrised with CHW data predicted DHW data.

Additionally, we drew the most likely posterior parameter set (defined by ABC-SMC) and visualised the most likely lethality build-up trajectories and the population survival trajectory under various regimes of the DHW experiment, with an emphasis on delineating sublethal effects induced by heatwaves.

2.6 | Assessing impacts of mesocosm-simulated heatwaves (DHWs) on recruitment and older-stage mussels

To relate the observed recruitment declines in mesocosms to the warming across DHW regimes, we employed Bayesian regression using the *brms* package (Bürkner, 2017). Our model incorporated a spline function to capture the logistic decline trend and assumed negative-binomial-distributed errors with a log-link function. We conducted parametrisation using four chains of 10,000 iterations each, including a 5000-iteration warmup period to ensure convergence.

To compare the severity of impacts on recruitment stages versus older stages (juveniles and adults), we assessed the correlation between the observed recruitment decline and the predicted average lethality build-up in older-stage mussels at the endpoint of the heatwaves. This comparison aims to provide a broader perspective on the differential sensitivity between stages, considering that mortalities in older stages were observed only at the warmest treatment levels.

2.7 | Projecting impacts of future extreme heatwaves on mussel population

Meier et al. (2021) provided every-other-day sea surface temperature projections for the Baltic Sea under the Representative Concentration Pathway 8.5 scenario throughout the 21st century. These projections indicated an increased frequency and duration of extremely warm events during summers, with peak temperatures reaching approximately 25°C near the entrance of Kiel Fjord (Coordinates: 54°26′55.9″N 10°15′45.2″E) located close to our study area (Figure S7). Preliminary observations suggested that local mussels could withstand temperatures up to 25°C for prolonged periods (exceeding 1 month). Consequently, we focused our research on evaluating the resilience of mussels against the five most severe projected summer scenarios.

To refine the bi-daily temperature projections to an hourly scale, we employed linear interpolation and developed a daily temperature fluctuation cycle. This cycle was based on hourly data collected from a shallow-water habitat in Kiel Fjord (1 m depth; Coordinates: 54°23′44.6″ N 10°11′27.5″ E) during the summer of 2019. We calculated the mean daily fluctuation by averaging the variations between the actual and average daily temperatures. These patterns were then integrated into our temperature projections.

We utilised the TTL model, optimised by applying ABC-SMC on DHW data, to project both individual lethality build-up trajectories and the corresponding population survival trajectory. For this, the temperature series for each extreme summer was input into the model, considering two scenarios with and without daily fluctuations (Figure S7).

Additionally, we used the average lethality build-up projected for older-stage mussels as a proxy for recruitment decline. Tracking survival duration and TTL modelling for recruitment stages was not feasible in this study. However, since both lethality build-up and recruitment are strongly driven by heat, we utilised the previously explained correlation to generate normalised recruit abundance predictions based on varying levels of average lethality build-up. This approach forms the basis for roughly projecting recruitment trends.

All computational methods were written and executed in the *R* programming language (version 4.2.3). All main scripts and data are accessible on the Zenodo-Github Repository: https://doi.org/10.5281/zenodo.12699002 (Vajedsamiei, 2024).

3 | RESULTS

In constant heatwave (CHW) regimes, survival of mussels (initial length range 7–20 mm) dropped to zero within 7 days at 29°C and 30 days at 28°C. At lower temperatures, survival probabilities were approximately 0.24 at 27°C and 0.75 at 26°C after 45 days. In the dynamic heatwave (DHW) experiment, declines in survival only occurred in the four highest temperature regimes. Survival rates dropped to zero within 52 days at a median temperature of 25.2°C (range 19.1–28.8°C). After 64 days, survival rates were 0.875, 0.825 and 0.325 at median temperatures of 23.8°C (19.4–27.4°C), 24.3°C (19.6–28.1°C) and 24.8°C (20.3–28.6°C), respectively. Detailed temperature statistics for all 12 DHW regimes are provided in Table S2.

3.1 | Thermal tolerance landscape (TTL) model validation

The thermal tolerance landscape (TTL) models parametrised by using approximate Bayesian computation via sequential Monte Carlo (ABC-SMC) on the dataset of each experiment exhibited high predictive accuracy when the same dataset was used for validation. The survival probabilities generated by the models closely aligned with the 95% confidence intervals of Kaplan–Meier curves from CHW or DHW experiments (Figure 2). We also obtained low mean absolute deviance (MAD) values, indicating a low disparity between survival predictions and the corresponding observed data (Table S3). For the CHW condition, the median MAD was 0.0572, with a 5th–95th percentile range of 0.0340 to 0.0758. Similarly, for the DHW condition, the median MAD was 0.0203, with a 5th–95th percentile range of 0.0104 to 0.0371. When the CHW data were used for ABC-SMC parameterisation of the TTL model and the DHW data were targeted for prediction, the model showed slightly less precise predictions, with a slightly higher median MAD of 0.0255 and a wider 5th–95th percentile range (0.0067 to 0.0629).

The Gaussian (bell-shaped) posterior distributions of the TTL parameters confirmed the successful sampling of the parameter spaces (Figure 3). Notably, we found no statistically significant effect of the heatwave type (CHW versus DHW) on the TTL model, as evidenced by overlapping 95% credible intervals (CI) of the distributions estimated by ABC-SMC on CHW and DHW datasets (Figure 3, the first two rows; Table S4). However, minor differences did exist, explaining why the TTL parametrised by ABC-SMC on CHW data could not predict DHW data with the same precision (described above).

Compared to ABC-SMC models, the TTL model parametrised by the Bayesian regression (BR) approach had less accuracy in predicting CHW data (median MAD: 0.0641, 5th–95th range: 0.0550–0.0744) and less accuracy in predicting DHW data (median MAD: 0.0469, 5th–95th range: 0.0370–0.0577) (Figures S9 and S10; Table S3). Expectedly, there were also major differences in the mean values of the parameter lethality build-up rate standard deviation ($SD(\dot{L}_r)$) and the parameter k, the latter denoted the temperature sensitivity of the lethality build-up rate (Figure 3; Table S4).

Based on the most probable posterior parameter set derived from the ABC-SMC approach within the TTL framework, we predicted the survival probability of the mussel population decreasing in response to the three warmest DHW treatment conditions (Figure 4). Concurrently, we predicted an accumulation of sublethal effects in mussel individuals (i.e. lethality build-up trajectories), occurring across a broader range of temperature treatments, not limited to the warmest ones. Over the five warmest DHW regimes, nearly all individuals of the populations were predicted to have >0.1 or >10% lethality build-up (Figure 4).

3.2 | Impacts of mesocosm-simulated heatwaves (DHWs) on recruits compared to older-stage mussels

The DHW experiment showed a logistic decline in the abundance of recruited (newly settled) mussels with the warming, with a sharp decrease at medium DHW levels (3°C above baseline), leading to near-zero recruitment at the highest DHW (Figure 5). The observed recruitment followed an exponential decay in correlation to the average lethality build-up predicted for older-stage mussels. The

Functional Ecology BRITISH ECOLOGICAL SOCIETY

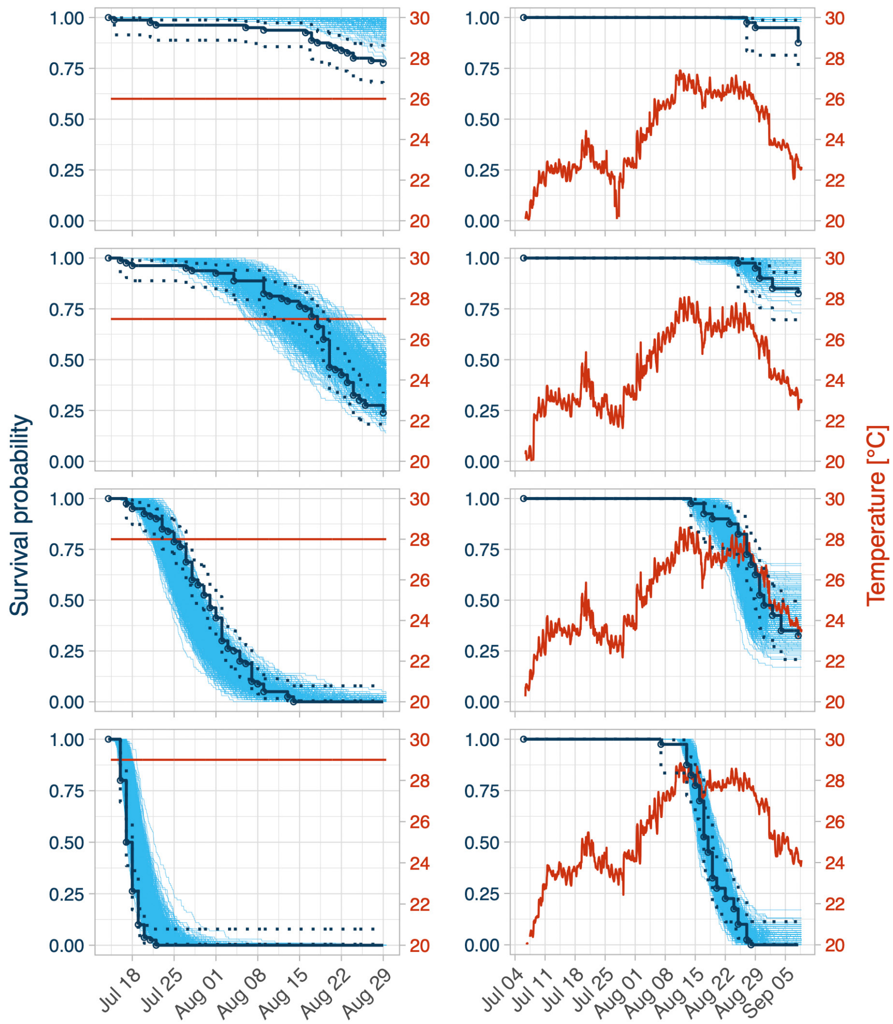

FIGURE 2 Predictive performance of the thermal tolerance landscape (TTL) model parametrised by using approximate Bayesian computation with sequential Monte Carlo (ABC-SMC) on the dataset from the constant heatwave (left column) or dynamic (right column) heatwave experiment. Posterior (likely) predictions of population survival trajectories (bright blue lines) are shown against the observed survival trajectory (dark blue circles) with corresponding interpolated Kaplan–Meier predictions (continuous dark blue lines) and their 95% confidence intervals (dotted lines). The thermal regimes experienced by the mussels are displayed in red.

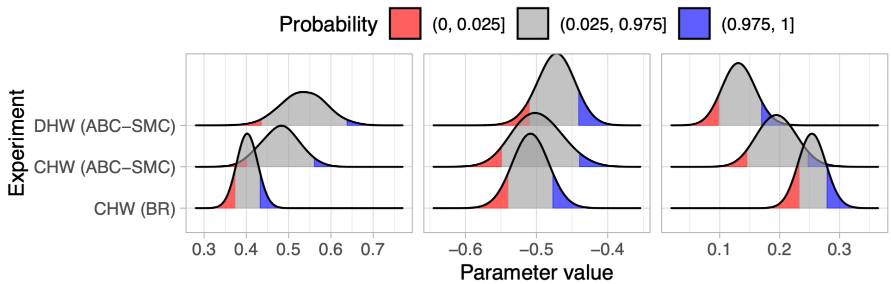

FIGURE 3 Posterior parameter distributions for the thermal tolerance landscape (TTL) model derived using approximate Bayesian computation via sequential Monte Carlo (ABC-SMC) and Bayesian Regression (BR) approaches on the data from constant and dynamic heatwave (CHW and DHW) experiments. The subplots, arranged from left to right, illustrate the distributions of the temperature sensitivity parameter *k*, and the mean and standard deviation of the lethality build-up rate at the reference temperature [mean$(\dot{L}_r)$ and SD$(\dot{L}_r)$, respectively], with $\dot{L}_r$ expressed on the decadic logarithm scale. The 95% credible intervals are represented in grey, and the lower and upper 2.5% probability quantiles are shown in red and blue, respectively. Note that the interval limits are approximate due to the bandwidth parameter used in the density plots, which introduces smoothing and can affect the precision of the interval boundaries. The exact statistics regarding the distributions are summarised in Table S4.

precise fit of the Bayesian regression models provided support for these associations (Figure 5). The latter correlation—though not indicative of a causal relationship—suggests that a low value of sublethal lethality build-up (e.g. ca. 25%) in older-stage mussels may signal a major recruitment drop (ca. 75%) (Figure 5).

3.3 | Projected effects of future extreme heatwaves on mussels

Our projection analysis, utilising the TTL model with the most likely parameter set obtained through ABC on data from the DHW

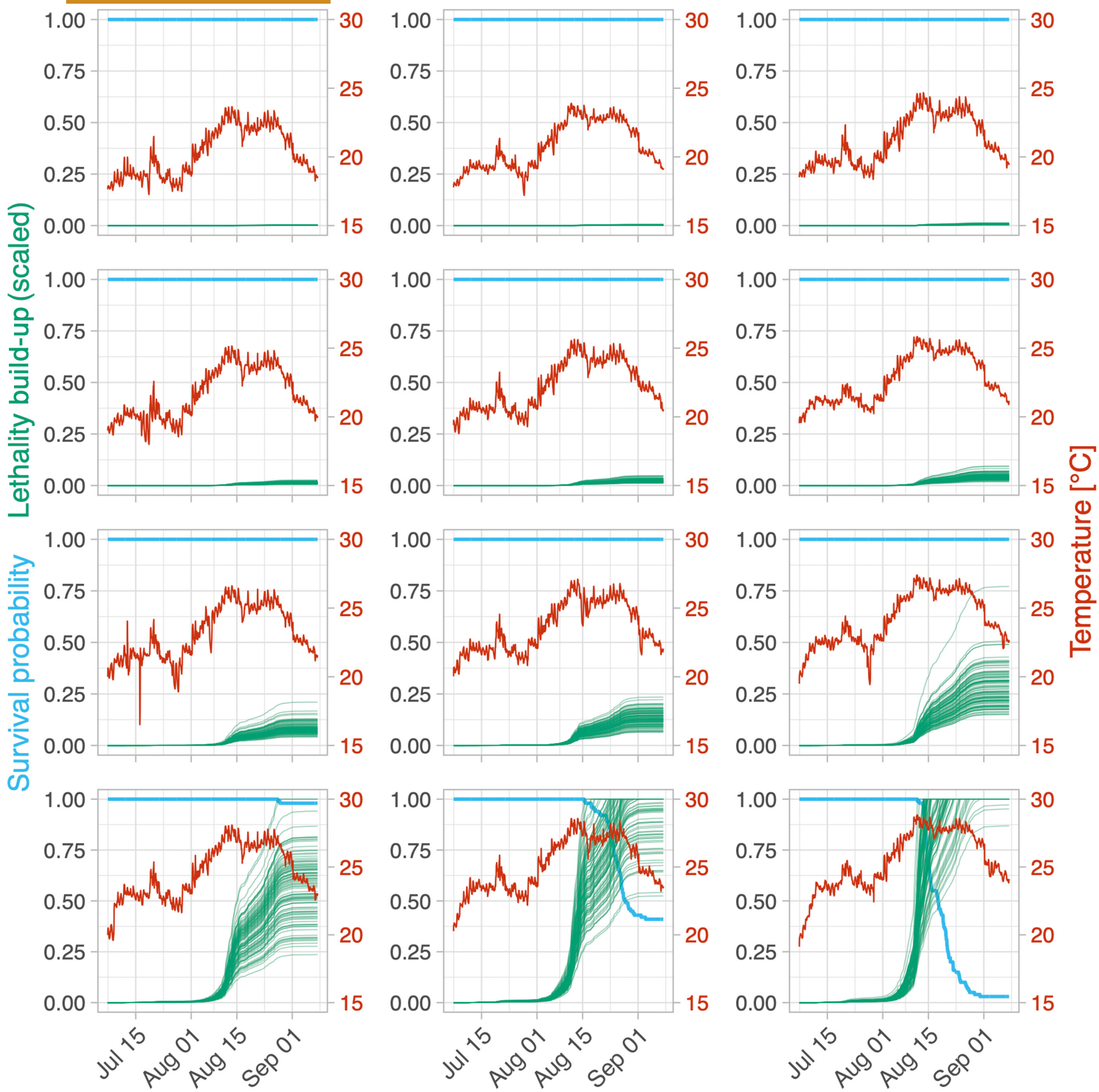

FIGURE 4 Most likely posterior predictions of survival trajectory (light blue lines) and scaled lethality build-up trajectories (green lines) for a mussel population subjected to twelve dynamic heatwave (DHW) regimes. The thermal tolerance landscape model was directly parametrised by applying approximate Bayesian computation via sequential Monte Carlo (ABC-SMC) on the data from the DHW experiment. The applied temperature regimes, indicated by the red lines, embody a wide range of thermal conditions under which we assessed mussel survival.

experiment, indicates that mussels (juveniles and adults) in the western Baltic Sea's shallow habitats may experience minor lethality build-up (<4%) under the warmest summer scenarios projected for this century, considering impacts of daily temperature fluctuations (Figure S11; Figure 6; Table S5). Considering the correlation described through the DHW experiment's findings, these minor impacts may signal 0% to ~34% decreases in recruitment, depending on the severity of the baseline temperature (Figure 6; Table S5). Notably, these rough projections assume that the median recruitment rate is capped at an optimum value of one.

4 | DISCUSSION

4.1 | ABC-SMC enabled probabilistic validation of TTL model assumptions

This study innovatively applied the approximate Bayesian computation with sequential Monte Carlo (ABC-SMC) method to probabilistically validate the assumptions underlying the thermal tolerance landscape (TTL) model. We defined TTL models for Baltic *Mytilus* mussels (adults and juveniles) by applying ABC-SMC

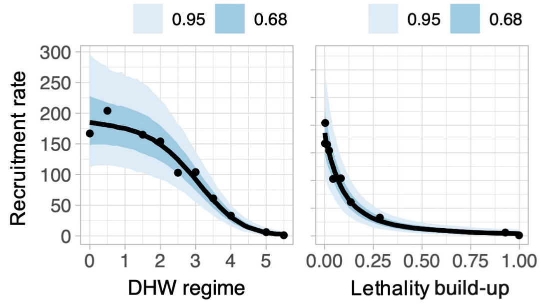

FIGURE 5 Impact of dynamic heatwave (DHW) regime on observed recruitment rate (left panel) and its correlation with modelled average lethality build-up (right panel). Points are the data used for establishing the Bayesian regression models, and shaded areas denote the 0.95 (light blue) and 0.68 (dark blue) credible intervals around the median predictions.

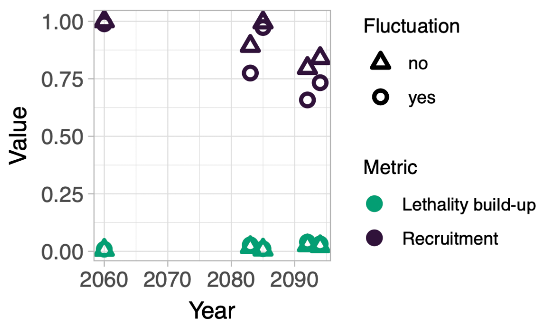

FIGURE 6 Projections of average lethality build-up in juvenile and adult mussels and a rough estimation of the correlated recruitment rates over the century's five warmest summer temperatures with and without daily fluctuations in the western Baltic Sea's shallow habitats. Lethality build-ups were projected using temperature projects by Meier et al. (2021) based on the Representative Concentration Pathway 8.5 scenario as input to the model parametrised by ABC-SMC on dynamic heatwave experiment data. The modelled lethality build-up was then used as a proxy for recruitment decline, according to the established correlation (Figure 5). All values are capped at one (the maximum rate).

separately to survival rate data from both mesocosm-simulated dynamic heatwave (DHW) events and laboratory-controlled constant heatwave (CHW) scenarios. The accuracy of the posterior distributions of the TTL models is evidenced by the small mean absolute deviance (MAD) between the posterior predictions and the observed data in both CHW and DHW experiments. These findings support the TTL assumption that survival durations (or their percent reciprocals: lethality build-up rates) at high temperatures vary among individuals and are exponentially related to temperature with a shared sensitivity exponent within the population. Additionally, the total lethality build-up can be quantified as a simple sum of the impacts over time (Fry et al., 1946; Jørgensen et al., 2019, 2021), with minimal compensatory acclimation effects (Havird et al., 2020; Vajedsamiei, Melzner, Raatz, Morón Lugo, & Pansch, 2021).

The assumption has been frequently supported by regression analyses examining the relationship between survival durations and constant temperatures (Bigelow, 1921; Fry et al., 1946; Jacobs, 1919) and by the ability of regression-based TTL models to provide predictions closely matching observed survival rates under dynamic temperature scenarios (Bertolini & Pastres, 2021; Fry et al., 1946; Jørgensen et al., 2021; Li et al., 2023; Rezende et al., 2020), suggesting the generalisability of the TTL assumptions across constant and dynamic settings. Our approach allowed us to test this in a probabilistic setting: the posterior parameter distributions estimated by ABC-SMC on CHW and DHW data showed only slight differences. Hence, the TTL model parametrised using ABC-SMC on CHW data could predict the DHW data with only a minor reduction in precision compared to the model directly parametrised using DHW data, suggesting the robustness and versatility of the TTL framework.

We also checked the predictive ability of a Bayesian regression (BR) within the TTL framework as an auxiliary analysis. Like ABC-SMC, BR allowed us to incorporate data from all constant temperatures, including censored data where not all individuals die within the experimental timeframe, an extended application over the frequentist regression approach. However, compared to ABC-SMC outcomes, the model parameterised via BR on CHW data showed less accuracy in predicting the CHW or DHW data.

4.2 | Recruitment and older-stage mussels differ in heat sensitivity but both may be resilient against this century's heatwaves

The ABC-SMC parametrisation also enabled the prediction of probable trajectories of lethality build-ups in juvenile and adult mussels during DHWs. As ectothermic animals, mussels exhibit intricate, temperature-sensitive physiological responses, encompassing modifications in metabolic rates, enzyme activities, cellular homeostasis, and gene expression patterns (Connor & Gracey, 2020; Georgoulis et al., 2022; Vajedsamiei, Melzner, Raatz, Kiko, et al., 2021). Under heightened temperatures, these alterations can lead to physiological setbacks, such as weakened immune functions (Cellura et al., 2007; Hong et al., 2021), reduced growth rates (Vajedsamiei, Melzner, Raatz, Morón Lugo, & Pansch, 2021), and perturbed reproduction (Béjaoui-Omri et al., 2014). The lethality build-up modelled in our study can quantitatively represent these sublethal effects and fitness setbacks.

The average predicted lethality build-up following heatwaves increased gradually across the warming treatments, ultimately surpassing 90% at the two highest temperature levels. In contrast, the observed recruitment rate in the same mesocosms showed a more pronounced decline with increasing temperature, exhibiting an exponential decrease in correlation with the increasing lethality build-up, though this is a non-causal relationship. Considering the developmental period of Baltic *Mytilus* larvae—typically lasting 3–5 weeks post-peak spring spawning—and the rapid water exchange rate in our mesocosm tanks, the settled larvae were sourced externally (Büttger et al., 2011; Seed, 1969; Thorarinsdóttir & Gunnarsson, 2003). Therefore, the observed decline in recruitment can be attributed to the adverse thermal effects on incoming larvae from the fjord during their critical final metamorphosis phase (late pelagic larvae) or on newly settled juveniles. Such impacts on the early life stages of ectotherms can have implications for the population dynamics and long-term survival of marine species under warming heatwave conditions (Collin et al., 2021; Sorte et al., 2011), which might be overlooked by the TTL predictions solely based on the heat sensitivity of older juveniles and adults.

Based on the TTL model with the most probable parameter set—obtained using the ABC-SMC on DHW data—we projected the resilience of juvenile and adult mussels in the western Baltic Sea's subtidal zones against the five most extreme summer temperatures projected for this century under high CO_2 emission scenarios (Meier et al., 2021). We projected no mortality and minor sublethal effects, even when wide daily temperature cycles were added to these extreme baselines. Considering our established correlation, these minor lethality build-ups would correspond to 0%–32% recruitment declines under these heatwaves. Considering the minor projected impacts of the five most severe scenarios, we would expect all less severe temperature projections to also have negligible effects on the mussel population.

We note that the surface temperature projection data used here were predominantly from open and deeper areas and may not fully capture thermal conditions in more restricted shallow waters where warmer heat waves may occur. Acknowledging this data gap and broadening our research scope is imperative.

Mytilus mussels exhibit high heat tolerance, potentially facilitated by their facultative anaerobic capability at temperatures above 25°C (Vajedsamiei, Melzner, Raatz, Morón Lugo, & Pansch, 2021), an adaptation acquired through evolutionary exposure to high-temperature environments. Previous studies have highlighted variability in heat tolerance among Baltic species (Pansch & Hiebenthal, 2019; van der Veer et al., 2006). For example, *Cerastoderma* bivalves lack anaerobic capability and demonstrate even greater heat resilience than *Mytilus*. In contrast, *Asterias* seastars, predators of *Mytilus*, show less heat tolerance (Rühmkorff et al., 2023). Extending TTL modelling to other key taxa can offer insights into future predator–prey dynamics and ecosystem stability in the face of climate change, with the caveat that this analysis assumes no adaptive changes in population thermal tolerances over time.

5 | CONCLUSIONS

This study enhanced TTL modelling using ABC-SMC, allowing direct TTL validation via survival data from dynamic, natural heatwave events. This approach yielded probabilistic predictions of sublethal impacts and mortality in the Baltic mussel population during experimental heatwaves. Mussels were much more susceptible to mesocosm-simulated heatwaves in their recruitment phase than in older juvenile and adult stages. Nevertheless, the model projected the overall resilience of mussels in the western Baltic Sea's shallow habitats against the most extreme summer temperatures projected for this century.

Envisioning the progression of this field, we propose several research directions:

1. Delineating the precise relationships between physiological responses and lethality build-up amidst heatwaves remains an area for future research, essential for decoding the temporal dynamics of mechanisms that culminate in mortality during such events.
2. Extending TTL model validation using heatwave survival data from monitoring programs of foundational coastal species, such as corals, or from aquaculture studies can help advance predictions for key marine populations facing escalating heatwaves.

AUTHOR CONTRIBUTIONS

J.V. formulated the method and the study design, performed data analysis and wrote the early manuscript. N.W. executed the experimental work. F.M. directed the community-level experiment at KOB and contributed to conceptual developments. H.E.M.M. provided processed climatic temperature projection data. All authors provided feedback and contributed to the final manuscript.

ACKNOWLEDGEMENTS

We thank Björn Buchholz for his attentive maintenance of the KOB system and for monitoring environmental conditions. This project was made possible through the support of the European Commission EU H2020-INFRAIA-2019-1-project (No. 871081) *AQUACOSM-plus*. Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST STATEMENT

We would like to confirm that there are no financial or personal relationships with any individuals or organisations that could inappropriately influence or bias our work as authors of this submission. We have thoroughly reviewed our affiliations, and there is no employment, consultancies, stock ownership, honoraria, paid expert testimony, patent applications/registrations, or grants or other funding to disclose in relation to this research. We provide this statement to affirm that there are no competing interests to declare among the authors of this manuscript.

DATA AVAILABILITY STATEMENT

Data and scripts supporting this study's findings are available from the Zenodo-Github Repository: https://doi.org/10.5281/zenodo.12699002 (Vajedsamiei, 2024).

ORCID

Jahangir Vajedsamiei https://orcid.org/0000-0002-8625-4719
H. E. Markus Meier https://orcid.org/0000-0001-5855-4645
Frank Melzner https://orcid.org/0000-0002-5884-1318

REFERENCES

Béjaoui-Omri, A., Béjaoui, B., Harzallah, A., Aloui-Béjaoui, N., El Bour, M., & Aleya, L. (2014). Dynamic energy budget model: A monitoring tool for growth and reproduction performance of *Mytilus*

galloprovincialis in Bizerte Lagoon (Southwestern Mediterranean Sea). *Environmental Science and Pollution Research*, *21*, 13081–13094.
Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, *15*, 365–377.
Bertolini, C., & Pastres, R. (2021). 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. *Estuarine, Coastal and Shelf Science*, *252*, 107284.
Bigelow, W. D. (1921). The logarithmic nature of thermal death time curves. *The Journal of Infectious Diseases*, *29*, 528–536.
Boutilier, R. G., & St-Pierre, J. (2000). Surviving hypoxia without really dying. *Comparative Biochemistry and Physiology. Part A, Molecular & Integrative Physiology*, *126*, 481–490.
Burge, C. A., Closek, C. J., Friedman, C. S., Groner, M. L., Jenkins, C. M., Shore-Maggio, A., & Welsh, J. E. (2016). The use of filter-feeders to manage disease in a changing world. *Integrative and Comparative Biology*, *56*, 573–587.
Bürkner, P.-C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, *80*, 1–28.
Büttger, H., Nehls, G., & Witte, S. (2011). High mortality of Pacific oysters in a cold winter in the North-Frisian Wadden Sea. *Helgoland Marine Research*, *65*, 525–532.
Cellura, C., Toubiana, M., Parrinello, N., & Roch, P. (2007). Specific expression of antimicrobial peptide and HSP70 genes in response to heat-shock and several bacterial challenges in mussels. *Fish & Shellfish Immunology*, *22*, 340–350.
Collin, R., Rebolledo, A. P., Smith, E., & Chan, K. Y. K. (2021). Thermal tolerance of early development predicts the realized thermal niche in marine ectotherms. *Functional Ecology*, *35*, 1679–1692.
Connor, K., & Gracey, A. Y. (2020). Cycles of heat and aerial-exposure induce changes in the transcriptome related to cell regulation and metabolism in *Mytilus californianus*. *Marine Biology*, *167*, 132.
Del Moral, P., Doucet, A., & Jasra, A. (2012). An adaptive sequential Monte Carlo method for approximate Bayesian computation. *Statistics and Computing*, *22*, 1009–1020.
Ern, R., Andreassen, A. H., & Jutfelt, F. (2023). Physiological mechanisms of acute upper thermal tolerance in fish. *Physiology*, *38*, 141–158.
Fry, F. E. J., Hart, J. S., & Walker, K. F. (1946). Lethal temperature relations for a sample of young speckled trout. *University of Toronto Studies. Biological Series*, *54*, 9–35.
Garrabou, J., Coma, R., Bensoussan, N., Bally, M., Chevaldonné, P., Cigliano, M., Diaz, D., Harmelin, J. G., Gambi, M. C., kersting, D. K., Ledoux, J. B., Lejeusne, C., Linares, C., Marschal, C., Pérez, T., Ribes, M., Romano, J. C., Serrano, E., Teixido, N., … Cerrano, C. (2009). Mass mortality in northwestern Mediterranean rocky benthic communities: Effects of the 2003 heat wave. *Global Change Biology*, *15*, 1090–1103.
Georgoulis, I., Bock, C., Lannig, G., Pörtner, H.-O., Feidantsis, K., Giantsis, I. A., Sokolova, I. M., & Michaelidis, B. (2022). Metabolic remodeling caused by heat hardening in the Mediterranean mussel Mytilus galloprovincialis. *The Journal of Experimental Biology*, *225*, jeb244795.
Gilbert, A. L., & Miles, D. B. (2017). Natural selection on thermal preference, critical thermal maxima and locomotor performance. *Proceedings of the Royal Society B: Biological Sciences*, *284*, 20170536.
Gomulkiewicz, R., & Holt, R. D. (1995). When does evolution by natural selection prevent extinction? *Evolution (N. Y.)*, *49*, 201–207.
Harley, C. D. G., Randall Hughes, A., Hultgren, K. M., Miner, B. G., Sorte, C. J. B., Thornber, C. S., Rodriguez, L. F., Tomanek, L., & Williams, S. L. (2006). The impacts of climate change in coastal marine systems. *Ecology Letters*, *9*, 228–241.
Havird, J. C., Neuwald, J. L., Shah, A. A., Mauro, A., Marshall, C. A., & Ghalambor, C. K. (2020). Distinguishing between active plasticity due to thermal acclimation and passive plasticity due to Q10 effects: Why methodology matters. *Functional Ecology*, *34*, 1015–1028.
Helmuth, B., Kingsolver, J. G., & Carrington, E. (2004). Biophysics, physiological ecology, and climate change: Does mechanism matter? *Annual Review of Physiology*, *67*, 177–201.
Hobday, A. J., Alexander, L. V., Perkins, S. E., Smale, D. A., Straub, S. C., Oliver, E. C. J., Benthuysen, J. A., Burrows, M. T., Donat, M. G., Feng, M., Holbrook, N. J., Moore, P. J., Scannell, H. A., Sen Gupta, A., & Wernberg, T. (2016). A hierarchical approach to defining marine heatwaves. *Progress in Oceanography*, *141*, 227–238.
Holbrook, N. J., Scannell, H. A., Sen Gupta, A., Benthuysen, J. A., Feng, M., Oliver, E. C. J., Alexander, L. V., Burrows, M. T., Donat, M. G., Hobday, A. J., Moore, P. J., Perkins-Kirkpatrick, S. E., Smale, D. A., Straub, S. C., & Wernberg, T. (2019). A global assessment of marine heatwaves and their drivers. *Nature Communications*, *10*, 1–13.
Hong, H.-K., Kim, C. W., Kim, J.-H., Kajino, N., & Choi, K.-S. (2021). Effect of extreme heatwaves on the mortality and cellular immune responses of purplish bifurcate mussel *Mytilisepta virgata* (Wiegmann, 1837) (=*Septifer virgatus*) in indoor mesocosm experiments. *Frontiers in Marine Science*, *8*, 794168.
Hughes, T. P., Barnes, M. L., Bellwood, D. R., Cinner, J. E., Cumming, G. S., Jackson, J. B. C., Kleypas, J., van de Leemput, I. A., Lough, J. M., Morrison, T. H., Palumbi, S. R., van Nes, E. H., & Scheffer, M. (2017). Coral reefs in the Anthropocene. *Nature*, *546*, 82–90.
IPCC. (2021). *Climate change 2021: The physical science basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press.
Jacobs, M. H. (1919). Acclimatization as a factor affecting the upper thermal death points of organisms. *The Journal of Experimental Zoology*, *27*, 427–442.
Jørgensen, L. B., Malte, H., Ørsted, M., Klahn, N. A., & Overgaard, J. (2021). A unifying model to estimate thermal tolerance limits in ectotherms across static, dynamic and fluctuating exposures to thermal stress. *Scientific Reports*, *11*, 12840.
Jørgensen, L. B., Malte, H., & Overgaard, J. (2019). How to assess *Drosophila* heat tolerance: Unifying static and dynamic tolerance assays to predict heat distribution limits. *Functional Ecology*, *33*, 629–642.
Larsson, J., Lind, E. E., Corell, H., Grahn, M., Smolarz, K., & Lönn, M. (2017). Regional genetic differentiation in the blue mussel from the Baltic Sea area. *Estuarine, Coastal and Shelf Science*, *195*, 98–109.
Laufkötter, C., Zscheischler, J., & Frölicher, T. L. (2020). High-impact marine heatwaves attributable to human-induced global warming. *Science (80-.)*, *369*, 1621–1625.
Li, Y.-J., Chen, S.-Y., Jørgensen, L. B., Overgaard, J., Renault, D., Colinet, H., & Ma, C. S. (2023). Interspecific differences in thermal tolerance landscape explain aphid community abundance under climate change. *Journal of Thermal Biology*, *114*, 103583.
Meier, H. E. M., Dieterich, C., & Gröger, M. (2021). Natural variability is a large source of uncertainty in future projections of hypoxia in the Baltic Sea. *Communications Earth & Environment*, *2*, 50.
Pansch, C., & Hiebenthal, C. (2019). A new mesocosm system to study the effects of environmental variability on marine species and communities. *Limnology and Oceanography: Methods*, *17*, 145–162.
Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., Clark, T. D., Colwell, R. K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R. A., Griffis, R. B., Hobday, A. J., Janion-Scheepers, C., Jarzyna, M. A., Jennings, S., … Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science (80-.)*, *355*, eaai9214.
Pinsky, M. L., Eikeset, A. M., McCauley, D. J., Payne, J. L., & Sunday, J. M. (2019). Greater vulnerability to warming of marine versus terrestrial ectotherms. *Nature*, *569*, 108–111.
Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., Brander, K., Bruno, J. F., Buckley, L. B., Burrows, M. T., Duarte, C. M., Halpern, B. S., Holding, J., Kappel, C. V., O'Connor, M. I., Pandolfi, J. M., Parmesan, C.,

Schwing, F., Thompson, S. A., & Richardson, A. J. (2013). Global imprint of climate change on marine life. *Nature Climate Change*, *3*, 919–925.

Pörtner, H. (2012). Integrating climate-related stressor effects on marine organisms: Unifying principles linking molecule to ecosystem-level changes. *Marine Ecology Progress Series*, *470*, 273–290.

Pörtner, H. O., Dupont, S., Melzner, F., Storch, D., & Thorndyke, M. (2010). Studies of metabolic rate and other characters across life stages. In U. Riebesell, V. Fabry, & J. P. Gattuso (Eds.), *Guide to best practices for ocean acidification research and data reporting* (pp. 167–180). Publications Office of the European Union.

Reusch, T. B. H., Dierking, J., Andersson, H. C., Bonsdorff, E., Carstensen, J., Casini, M., Czajkowski, M., Hasler, B., Hinsby, K., Hyytiäinen, K., Johannesson, K., Jomaa, S., Jormalainen, V., Kuosa, H., Kurland, S., Laikre, L., MacKenzie, B. R., Margonski, P., Melzner, F., … Zandersen, M. (2018). The Baltic Sea as a time machine for the future coastal ocean. *Science Advances*, *4*, eaar8195.

Rezende, E. L., Bozinovic, F., Szilágyi, A., & Santos, M. (2020). Predicting temperature mortality and selection in natural *Drosophila* populations. *Science (80-.)*, *369*, 1242–1245.

Rezende, E. L., Castañeda, L. E., & Santos, M. (2014). Tolerance landscapes in thermal ecology. *Functional Ecology*, *28*, 799–809.

Rubin, D. B. (1984). Bayesianly justifiable and relevant frequency calculations for the applied statistician. *The Annals of Statistics*, *12*, 1151–1172.

Rühmkorff, S., Wolf, F., Vajedsamiei, J., Barboza, F. R., Hiebenthal, C., & Pansch, C. (2023). Marine heatwaves and upwelling shape stress responses in a keystone predator. *Proceedings of the Royal Society B: Biological Sciences*, *290*, 20222262.

Seed, R. (1969). The ecology of *Mytilus edulis* L. (Lamellibranchiata) on exposed rocky shores: I. Breeding and settlement. *Oecologia*, *3*, 277–316.

Seuront, L., Nicastro, K. R., Zardi, G. I., & Goberville, E. (2019). Decreased thermal tolerance under recurrent heat stress conditions explains summer mass mortality of the blue mussel *Mytilus edulis*. *Scientific Reports*, *9*, 17498.

Sisson, S. A., Fan, Y., & Tanaka, M. M. (2007). Sequential Monte Carlo without likelihoods. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 1760–1765.

Skirving, W. J., Heron, S. F., Marsh, B. L., Liu, G., De La Cour, J. L., Geiger, E. F., Mark Eakin, C., & De La Cour, J. (2019). The relentless march of mass coral bleaching: A global perspective of changing heat stress. *Coral Reefs*, *38*, 547–557.

Sokolova, I. M. (2023). Ectotherm mitochondrial economy and responses to global warming. *Acta Physiologica*, *237*, e13950.

Somero, G. N. (2010). The physiology of climate change: How potentials for acclimatization and genetic adaptation will determine "winners" and "losers". *The Journal of Experimental Biology*, *213*, 912–920.

Sorte, C. J. B., Jones, S. J., & Miller, L. P. (2011). Geographic variation in temperature tolerance as an indicator of potential population responses to climate change. *Journal of Experimental Marine Biology and Ecology*, *400*, 209–217.

Strydom, S., Murray, K., Wilson, S., Huntley, B., Rule, M., Heithaus, M., Bessey, C., Kendrick, G. A., Burkholder, D., Fraser, M. W., & Zdunic, K. (2020). Too hot to handle: Unprecedented seagrass death driven by marine heatwave in a world heritage area. *Global Change Biology*, *26*, 3525–3538.

Thorarinsdóttir, G. G., & Gunnarsson, K. (2003). Reproductive cycles of *Mytilus edulis* L. on the west and east coasts of Iceland. *Polar Research*, *22*, 217–223.

Vajedsamiei. (2024). jvajedsamiei/A-Bayesian-overhaul-of-thermal-tolerance-landscape-models: A Bayesian Overhaul of Thermal Tolerance Landscape Models (ABC-SMC). *Zenodo*, https://doi.org/10.5281/zenodo.12699002

Vajedsamiei, J., Melzner, F., Raatz, M., Kiko, R., Khosravi, M., & Pansch, C. (2021). Simultaneous recording of filtration and respiration in marine organisms in response to short-term environmental variability. *Limnology and Oceanography: Methods*, *19*(3), 196–209.

Vajedsamiei, J., Melzner, F., Raatz, M., Morón Lugo, S. C., & Pansch, C. (2021). Cyclic thermal fluctuations can be burden or relief for an ectotherm depending on fluctuations' average and amplitude. *Functional Ecology*, *35*(11), 2483–2496.

Vajedsamiei, J., Wahl, M., Schmidt, A. L., Yazdanpanahan, M., & Pansch, C. (2021). The higher the needs, the lower the tolerance: Extreme events may select ectotherm recruits with lower metabolic demand and heat sensitivity. *Frontiers in Marine Science*, *8*, 264.

van der Veer, H. W., Cardoso, J. F. M. F., & van der Meer, J. (2006). The estimation of DEB parameters for various Northeast Atlantic bivalve species. *Journal of Sea Research*, *56*, 107–124.

Wahl, M., Buchholz, B., Winde, V., Golomb, D., Guy-Haim, T., Müller, J., Rilov, G., Scotti, M., & Böttcher, M. E. (2015). A mesocosm concept for the simulation of near-natural shallow underwater climates: The Kiel Outdoor Benthocosms (KOB). *Limnology and Oceanography: Methods*, *13*, 651–663.

Wernberg, T., Bennett, S., Babcock, R. C., de Bettignies, T., Cure, K., Depczynski, M., Dufois, F., Fromont, J., Fulton, C. J., Hovey, R. K., Harvey, E. S., Holmes, T. H., Kendrick, G. A., Radford, B., Santana-Garcon, J., Saunders, B. J., Smale, D. A., Thomsen, M. S., Tuckett, C. A., … Wilson, S. (2016). Climate-driven regime shift of a temperate marine ecosystem. *Science (80-.)*, *353*, 169–172.

Zippay, M. L., & Helmuth, B. (2012). Effects of temperature change on mussel, *Mytilus*. *Integrative Zoology*, *7*, 312–327.

Zittier, Z. M. C., Bock, C., Lannig, G., & Pörtner, H. O. (2015). Impact of ocean acidification on thermal tolerance and acid–base regulation of *Mytilus edulis* (L.) from the North Sea. *Journal of Experimental Marine Biology and Ecology*, *473*, 16–25.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Text S1: Rationale for using the term *lethality buildup rate*.

Text S2: ABC: Origins, extensions, and applications.

Text S3: General description of the ABC-SMC approach for TTL model parametrization (as implemented in the *R* script).

Text S4: Bayesian regression (BR) analysis on data from constant heatwave (CHW) experiment.

Figure S1: Schematic of setups for the constant heatwave (CHW) and dynamic heatwave (DHW) experiments.

Figure S2: Shell length distribution of *Mytilus* mussels of the two size classes at the end of the constant heatwave (CHW) and dynamic heatwave (DHW) experiments.

Figure S3: Hourly temperature profiles across various treatments (0 to 5.5) during the dynamic heatwave (DHW) experiment, along with natural Kiel fjord conditions, recorded from mid-July to early September.

Figure S4: Association of temperature datasets for all experimental treatments alongside fjord conditions, showing GHL sensor recordings (lines) supplemented with hourly data collected by Hach sensor (Dissolved Oxygen Sensor, Hach Lange GmbH, Germany), for missing intervals, against corroborative WTW sensor measurements (circles).

Figure S5: Daily recorded values of oxygen saturation, pH, and salinity, along with weekly measurements of chlorophyll-*a* concentrations, across all treatment levels of the dynamic heatwave (DHW) experiment and fjord conditions.

Figure S6: Survival trajectories of large and small *Mytilus* mussels under the treatments reflecting both constant (CHW) and dynamic heatwave (DHW) conditions, designated by the identifiers 26, 27, 28, 29 for CHW, and 4, 4.5, 5, 5.5 for DHW, respectively.

Figure S7: Projections of summer temperatures for the current century at the Kiel Fjord entrance site under the Representative Concentration Pathway 8.5 scenario were refined to an hourly scale (left side plot).

Figure S8: Posterior predictions of the Bayesian log-linear regression modeling of the lethality buildup rate ($\dot{L}$; at log10 scale) over constant temperatures and the observations (dots).

Figure S9: Monte Carlo simulation of mussel survival probabilities at constant or dynamic heatwave regimes (left versus right-side columns) based on the whole posterior parameter sets from the Bayesian regression (see Text S3).

Figure S10: Distributions of the mean absolute deviance (MAD) for constant heatwave (CHW) and dynamic heatwave (DHW) experiments across various treatment levels.

Figure S11: Projected survival and mean lethality buildup for mussels under five warmest summer temperature regimes projected for the years 2060, 2083, 2085, 2092, and 2094 (top to bottom), considering scenarios with and without daily temperature fluctuations (left versus right-side subplots).

Table S1: Cox proportional hazards model analysis detailing the effects of size class and temperature treatment on *Mytilus* mussel survival across constant (CHW) and dynamic (DHW) heatwave experiments.

Table S2: Summarized temperature regimes applied in the 64-day dynamic heatwave (DHW) experiment are characterized by various temperature statistics, including the median, 5th and 95th percentiles, mean, standard deviation (SD), minimum (min), and maximum (max) temperatures [°C].

Table S3: Comparison of the mean absolute deviance (MAD) in survival rate simulations for different methods of Thermal Tolerance Landscape model parameterization and experimental data.

Table S4: Summary statistics of Thermal Tolerance Landscape (TTL) model parameters estimated by an Approximate Bayesian Computation-Sequential Monte Carlo (ABC-SMC) and Bayesian Regression (BR) approaches for two experimental conditions: constant heatwave (CHW) and dynamic heatwave (DHW) regimes.

Table S5: Projected average lethality buildup (Average *L*) and recruitment probabilities (50th, 95th, and 5th percentiles) under the five warmest projected summer regimes, with and without daily fluctuations.

How to cite this article: Vajedsamiei, J., Warlo, N., Meier, H. E. M., & Melzner, F. (2024). Predicting key ectotherm population mortality in response to dynamic marine heatwaves: A Bayesian-enhanced thermal tolerance landscape approach. *Functional Ecology*, *38*, 1875–1887. https://doi.org/10.1111/1365-2435.14620