

RESEARCH ARTICLE

Marine Heatwaves

Predicting organismal response to marine heatwaves using dynamic thermal tolerance landscape models

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Abstract

1. Marine heatwaves (MHWs) can cause thermal stress in marine organisms, experienced as extreme 'pulses' against the gradual trend of anthropogenic warming. When thermal stress exceeds organismal capacity to maintain homeostasis, organism survival becomes time-limited and can result in mass mortality events.
2. Current methods of detecting and categorizing MHWs rely on statistical analysis of historic climatology and do not consider biological effects as a basis of MHW severity. The re-emergence of ectotherm thermal tolerance landscape models provides a physiological framework for assessing the lethal effects of MHWs by accounting for both the magnitude and duration of extreme heat events.
3. Here, we used a simulation approach to understand the effects of a suite of MHW profiles on organism survival probability across (1) three thermal tolerance adaptive strategies, (2) interannual temperature variation and (3) seasonal timing of MHWs.
4. We identified survival isolines across MHW magnitude and duration where acute (short duration-high magnitude) and chronic (long duration-low magnitude) events had equivalent lethal effects on marine organisms. While most research attention has focused on chronic MHW events, we show similar lethal effects can be experienced by more common but neglected acute marine heat spikes. Critically, a statistical definition of MHWs does not accurately categorize biological mortality.
5. By letting organism responses define the extremeness of a MHW event, we can build a mechanistic understanding of MHW effects from a physiological basis. Organism responses can then be transferred across scales of ecological organization and better predict marine ecosystem shifts to MHWs.

KEY WORDS

climate change, ecological forecasting, ecophysiology, extreme events, heat stress, mass mortality events, mechanistic ecological models, thermal tolerance

1 | INTRODUCTION

With the acceleration of climate change has come an urgent need to understand impact pathways on marine ecosystems. Extreme events are hypothesized to have stronger impacts on organisms

than shifts in mean climate conditions (Bailey & van de Pol, 2016; Harris et al., 2018). The increased frequency, intensity and duration of marine heatwaves (MHWs) have garnered attention as a symptom of climatic warming (Frölicher et al., 2018; Oliver et al., 2021). Like many physical stressors, MHWs are composed of discrete pulses of

magnitude and duration against the background of chronic warming (Harris et al., 2018). Extreme events due to weather stochasticity are naturally occurring, but as climate change presses temperature distributions upwards these events become more prevalent and increase the probability of lethal effects on organisms (Frölicher et al., 2018; Harvey et al., 2022; Scheffer et al., 2001; Smale et al., 2019). Mass mortality events (MMEs) occur when a population of organisms can no longer maintain physiological homeostasis or function (Ern et al., 2023; Ørsted et al., 2022) and are potential sources of phase shifts in population dynamics. Most studies investigating MHW-linked MMEs are descriptive field studies (Fey et al., 2015; Garrabou et al., 2022; Glynn, 1968; Jurgens et al., 2015; Raymond et al., 2022; Tricklebank et al., 2021) that do not investigate how different MHW profiles contribute to MME extent. Newer experimental methods have incorporated more realistic MHW profiles by matching temperature simulations in mesocosms to real-world conditions and treating dimensions of variability as themselves predictors of interest (Gerhard et al., 2023; Jentsch et al., 2007; Pansch et al., 2018). For example, exposing *Mytilus edulis* mussels to multiple heat events in the lab more closely approximated observed field mortality (Seuront et al., 2019), and temperate macroalgae in mesocosms showed divergent responses to the interactions of baseline warming and upwelling timing (Wahl et al., 2021). Despite these experimental allowances for realistic variation, prediction of biological effects from in situ MHWs remains elusive.

MHW extremeness can be defined using the climatological context in which they occur (Bailey & van de Pol, 2016; Hobday et al., 2016). Recent work has defined MHWs as discrete periods when temperatures exceed a seasonally varying threshold, which usually is represented by the 90th percentile of historical climatology for five or more consecutive days (Hobday et al., 2016, 2018; Oliver et al., 2021). This 90th percentile is calculated daily and thus varies seasonally, which is relevant in the context of many organisms' phenology and performance throughout a seasonally variable environment (Hobday et al., 2016). Additionally, MHW severity can be categorized to allow for comparison between events of varying intensity, duration and rate of onset (Hobday et al., 2018), although explicit categorization is determined by intensity only. This approach quantifies extreme conditions within a local spatiotemporal context and approximates what is likely considered extreme by organisms (Oliver et al., 2021).

While such a fixed baseline statistical metric can be a good tool for understanding broad patterns, it does not provide a clear picture of how extreme heat differentially affects organisms. For example, organism abilities to withstand MHWs vary greatly depending on physiology, behaviour, function and available thermal microclimates within an environment (Dong, 2023; Harris et al., 2018; Smith et al., 2023). Further, a statistical definition of MHWs is only relevant when long-term data are available at the scale relevant to an organism, which can vary widely from millimetres to thousands of kilometres (Bates et al., 2018; Helmuth, 2009; Helmuth et al., 2006). Finally, a five-day minimum threshold duration for a MHW ignores extreme heat events that can occur on much shorter timescales in marine

systems and result in real biological effects (Bates et al., 2018; White et al., 2023). For example, coastal and intertidal species can be subjected to statistically extreme conditions over diel tidal fluctuations due to the complexity of solar heating, water residence time, microhabitat orientation and upwelling (Davis et al., 2011; Denny & Paine, 1998; Helmuth et al., 2006; Reid et al., 2020). Adhering exclusively to a statistical definition of MHWs fails to consider biological responses to these context-dependent events (Smith et al., 2023). Conversely, experiments and models that describe physiological responses to temperature rarely capture variability found in MHWs and rely on responses to mean conditions, thereby ignoring non-linear responses and the effects of Jensen's inequality (Buckley & Kingsolver, 2021; Dowd et al., 2015; Gerhard et al., 2023; Harris et al., 2018; Morash et al., 2018). To these ends, we lack coherent models that mechanistically link MHWs to observed responses in organisms and ecosystems (González-Trujillo et al., 2023; van de Pol et al., 2017).

A mechanistic model of organism mortality in response to MHWs needs to accommodate variation in the magnitude (or intensity) and duration of a heat challenge. Existing metrics that account for heat duration include cumulative intensity metrics, such as those used in remote-sensed coral reef bleaching tracking products (e.g. Coral Reef Watch, Heron et al., 2016; McClanahan, 2022; Skirving et al., 2020). However, such approaches still rely on static thresholds over which stress accumulation is calculated. A significant mechanistic development towards predicting the lethal effects of MHWs has been the re-emergence of the thermal death time (TDT) model of ectotherm thermal tolerance—a model that predicts death as a function of thermal exposure magnitude and time (Rezende et al., 2014). This model conceptualizes thermal challenge as a heat-dose, and better unifies the relationship between duration and magnitude of exposure that occur in MHWs (Neuner & Buchner, 2023). When these TDT curves are combined with survival probability functions, a thermal tolerance landscape is produced which calculates survival probability as a continuous response to temperature and temporal exposure (Rezende et al., 2014). Dynamic tolerance models can be built around thermal tolerance landscapes (Rezende et al., 2020) or TDT curves (Jørgensen et al., 2021) to predict survival over varying temperature exposures within an organism's environment. Dynamic tolerance models therefore account for time-dependent effects of heat stress. An important prediction of these models is death at relatively benign temperatures and extended temporal exposures, which are generally unaccounted for in single measures of thermal tolerance such as CT_{max} and LT_{50} . Therefore, dynamic tolerance models may identify cryptic mortality events that are not predicted by static thermal tolerance indices.

The dynamic tolerance model approach produces more accurate predictions of organism mortality within an environmental context than single measures of thermal tolerance, and has shown promise in scaling up physiological effects of climate change to population and community dynamics. Dynamic tolerance models predicted mortality events with current and future water temperature scenarios in Venice Lagoon bivalves (Bertolini et al., 2023), Antarctic marine

invertebrates (Carter et al., 2023; Molina et al., 2022), and riverine amphipods (Verberk et al., 2023). There has been a single application of dynamic tolerance models to MHWs that investigated the potential for mismatches between statistical MHW categorization and modelled mortality. Bertolini and Pastres (2021) predicted occasions when clams (*Ruditapes philippinarum*) in the Venice lagoon exhibit no mortality during several statistically-defined heatwaves, while conversely thermal mortality was predicted during non-MHW conditions. Such mismatches signal a decoupling between statistical categorization of MHW events and subsequent biological responses.

Here, we present a generalized MHW simulation to understand how organism mortality responds to variation in MHW duration and magnitude, and how a dynamic tolerance approach compares to Hobday's fixed-baseline categorization of MHW extremity. We first simulate a suite of simple MHWs that vary in magnitude and duration following the threshold-duration definition of Hobday et al. (2016) to explore MHW possibilities relative to a long-term climatological baseline. We then simulate the exposure of three hypothetical organisms with different thermal strategies to each MHW time series using dynamic tolerance models and extract final probability estimates of mortality. We show how categorizing MHWs from the resulting survival landscape results in a biologically informed assessment of MHW lethal impacts that can better guide ad hoc classifications of MHW impacts. We hypothesize that similar levels of mortality can occur across MHW climatology categories and levels of variability within an environment, which may mean a statistical definition of MHWs can both over- and under-estimate ecosystem impacts depending on interannual variability. Furthermore, a biological approach will correctly predict low mortality from MHWs occurring during cooler seasons.

2 | METHODS

2.1 | Simulation of MHW profiles

We first constructed a suite of MHWs with varying magnitude and duration parameters. Hobday et al. (2016) define three main MHW components: magnitude (thermal intensity), duration (temporal length of MHW above 90th percentile) and rate of onset/decline (slope value between maximum intensity and beginning/end of climatological heatwave; Figure 1a). We defined duration as the MHW length as it departs from the climatological curve, not the 90% threshold. We adopted this definition because we simulated our time series as sinusoidal curves with no stochastic component, focusing on the main effect of an idealized MHW. We did not manipulate rate of onset/decline as an independent parameter of magnitude and duration, as this would require introducing a second MHW geometry (trapezoidal) and is not aligned with our main research questions.

We simulated MHWs that ranged in duration from 1 h to 30 days, with a timestep of 1 day. We investigated MHW duration shorter than the Hobday et al. (2016) threshold of 5 days (marine heat spikes) because of several case studies of organism mortality in extreme heat conditions that lasted less than 5 days (Bates et al., 2018; Glynn, 1968; Raymond et al., 2022). Next, we simulated MHWs ranging in magnitude from 0 to 8°C with discrete breaks of 0.5°C. We chose 8°C as our maximum magnitude, as this encapsulates the magnitudes of the most intense observed MHWs (Hobday et al., 2018; Holbrook et al., 2019), although see Figure S1 for additional MHW magnitudes. In total, we simulated 527 distinct MHW profiles across magnitude-duration parameters.

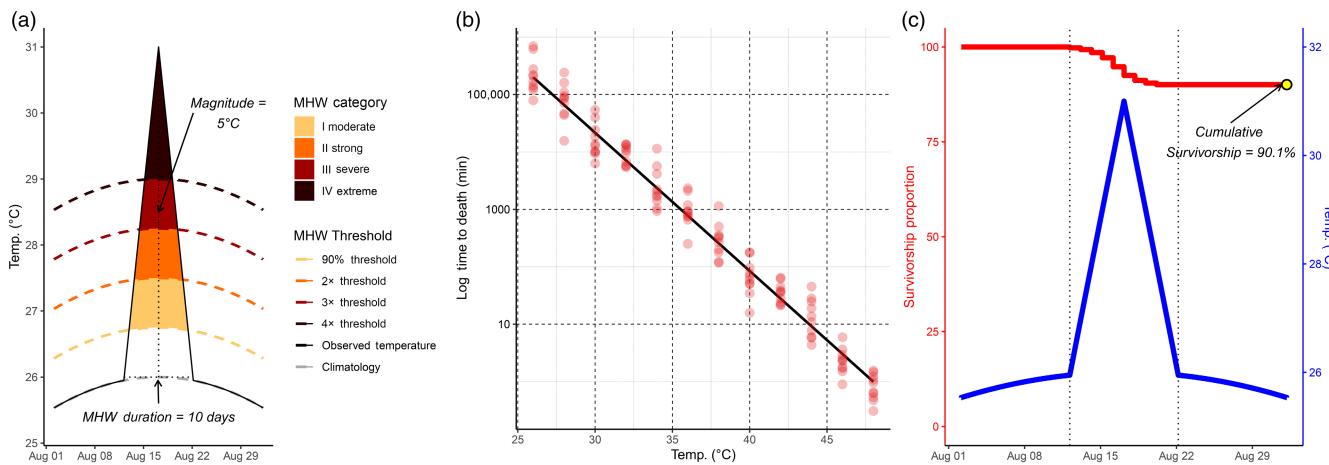


FIGURE 1 Conceptual diagram of survival calculation over a marine heatwave (MHW) simulation using thermal death time (TDT) curves and dynamic tolerance models. (a) A simulated MHW displaying magnitude (5°C) and duration (10 days) parameters (black dotted lines). Coloured dashed lines indicate MHW severity thresholds, and coloured areas the portion of the MHW profile within MHW categories. This MHW is a category IV 'extreme' under the Hobday definition. Climatology line (grey) indicates the historical time series over which thresholds are calculated. The 90% threshold is defined here as +0.75°C above climatology. (b) A TDT curve for a hypothetical species of $CT_{max}=48^{\circ}\text{C}$, $z=4.15$ (acute tolerator, Figure 2a). The line of fit is determined via linear regression on logarithmically transformed data. Points are simulated data (see Section 2). (c) The temperature time series from (a) and the thermal tolerance landscape in (b) are the inputs of a dynamic tolerance model that gives a single survival probability estimate of 90.1% for the given MHW parametrization of magnitude and duration. Dotted vertical lines indicate the beginning and end of the MHW.

We added each MHW to 52 days of a simulated temperature time series, composed of a sinusoidal curve with an annual mean of 12°C and an annual variation of 14°C (min = -2°C, max = 26°C). Annual time series maxima occurred on August 17th, and minima on February 15th. This approximates temperature profiles found in temperate estuarine environments in the northern hemisphere. We next added three thresholds on top of this curve, representing scenarios where 90% of interannual temperature variation occurred within 0.25°C, 0.75°C (threshold used in conceptual diagram, [Figure 1a](#)), and 1.5°C above annual mean temperature (climatology). Using the MHW categorization developed by Hobday et al. ([2018](#)), we assigned three additional thresholds for each variation scenario that were 1x, 2x, 3x, and 4x the difference between climatology and the 90% MHW threshold to give moderate, strong, severe and extreme categorizations ([Figure 1a](#)).

To further demonstrate seasonal timing effects on acute tolerator survival from MHWs, we simulated MHWs across 10 time points 90 days after the annual maximum on August 17. We created MHWs with magnitude ranging between 0°C and 8°C but fixed duration at 24 days. We set the 90% threshold at 0.75°C above the climatological mean. In total, we simulated 2788 unique temperature time series across three species (1581 simulations), seasonal variability (1054 simulations) and seasonal timing (153 simulations).

2.2 | Simulation of thermal death time curves

Thermal death time (TDT) curves model the time-dependent effects of temperature exposure on organismal thermal tolerance (Rezende et al., [2014](#)). Time to death at a given temperature is determined by a log linear relationship with temperature of exposure:

$$\log_{10} t = \frac{(CT_{max} - T_{assay})}{z}, \quad (1)$$

where t is the time to knockdown (or death), CT_{max} is the acute thermal tolerance at $\log_{10} t = 0$, which by definition is the thermal tolerance at 1 min of exposure, z is a scaling constant representing the inverse slope of the relationship between temperature and log time, and T_{assay} is assay temperature (°C) ([Equation 1, Figure 1b](#)). From each TDT curve and the empirical measures of time to death that it describes, we constructed thermal tolerance landscapes. These landscapes start from the assumption that a TDT curve is simply a 50% survival isocline, and the spread of empirical time to death for a given temperature can be used to construct additional mortality probability isoclines (Rezende et al., [2014](#)). Combining survival isoclines together results in a three-dimensional thermal tolerance landscape that fully describes the continuous interactions of time and temperature exposure on probability of death (Rezende et al., [2014](#)).

We simulated three hypothetical species' TDT models with different parameter sets that reflect three hypothetical thermal adaptation strategies ([Figure 2a](#)). We simulated a chronic tolerator organism that maximizes extended exposure tolerance ($z = 2.75$) against a trade-off of low acute tolerance ($CT_{max} = 44^\circ\text{C}$), and an

acute tolerator that maximizes acute tolerance ($CT_{max} = 48^\circ\text{C}$) at the expense of rapidly decaying tolerance over time ($z = 4.15$). Finally, we simulated a 'mixed strategy' species that had the same acute tolerance as the chronic tolerator ($CT_{max} = 44^\circ\text{C}$) but a more rapid loss of tolerance with exposure time ($z = 3.23$). We selected parameter values such that the acute and chronic species TDT curves intersect at 30 h and 36.1°C, the chronic and mixed strategy species at 1 min and 44°C, and the acute and mixed strategy species at 15 days and 30°C ([Figure 2a](#)). The temperature at which any two strategies have equal responses occurs at their TDT curve intersection. We note that since the baseline for our MHW simulations is 26°C and the maximum MHW simulated is 34°C (8°C above baseline), only the intersection of the acute and mixed strategy species (30°C, 15 days) is observable in our result heatmaps. This is intentional, so as to demonstrate that putatively tolerant species only outperform other species at extreme temperatures over short intervals (but see [Figure S1](#) for additional MHW magnitudes, 8–20°C). While these values are not taken from actual species, they do approximate values of temperate marine bivalve species such as *Cerastoderma glaucum* and *Donax trunculus* (Ansell et al., [1980, 1981](#)).

Using the z and CT_{max} parameters for each hypothetical species, we simulated empirical time to death for each species' log-linear model. We simulated 10 individuals per temperature treatment (26–48°C, by 2°C, total of 12 temperature treatments) following a normal distribution wherein mean time to death occurred at the line of fit and error given as standard error = 0.1°C ([Figure 2a](#)).

2.3 | Implementation of dynamic tolerance models

Dynamic tolerance models integrate TDT data and environmental temperature time series to give a cumulative survival estimate at the end of the time series ([Figure 1c, Supporting Information](#)). We added an additional parameter within our ad hoc functions adapted from the Rezende model (Rezende et al., [2020](#)) to account for the proposed critical temperature (T_c) delineating the limit of organismal maintenance of homeostasis and function (see [Supporting Information](#); Jørgensen et al., [2021](#); Ørsted et al., [2022](#); Pörtner, [2010](#)). In our simulation, we set $T_c = 26^\circ\text{C}$ as this is the maximum climatological temperature experienced by our hypothetical organisms. Additionally, we assumed no nightly or tidal immersion stress recovery of organisms during each MHW because each simulation is continuous over its duration, regardless of potential diel cycles. We calculated cumulative mortality for each MHW simulation and extracted the survival at the end of the exposure period ([Figure 1c](#)) using the Rezende dynamic tolerance model parameterized by one of the three hypothetical species TDT curves (Rezende et al., [2020](#)). In addition, we used adjusted functions to accommodate hourly time series from the heatwaveR package (Schlegel & Smit, [2018](#)) to categorize each simulated MHW according to the statistical, oceanographic definition (Hobday et al., [2018](#)). We performed all analyses in R (v. 4.2.2). We did not need animal care ethical approval due to the simulation nature of the analysis.

3 | RESULTS

The heatmap of survival between three hypothetical species revealed a substantial impact of different TDT curve adaptations on survival across simulated MHWs. The acute tolerator (high CT_{max} , high z) experienced higher mortality across all simulations compared to the chronic tolerator (low CT_{max} , low z ; Figure 2b). The mixed-strategy species exhibited less mortality than the acute tolerator at duration and magnitude combinations lower than their TDT curve point of intersection at 15 days and 30°C (Figure 2a), but for magnitude and duration combinations beyond this point mortality rate in the mixed strategy species accelerates. This results in a steeper decline in survival for the mixed-strategy species, such that at the most extreme magnitude-duration combination mortality is comparatively larger than the acute tolerator (Figure 2b). The two other intersection points (acute-chronic, 30h 36.1°C and chronic-mixed, 1 min 44°C, Figure 2a) are not visible

on the heatmap because they occur at short time scales and/or extreme temperatures (Figure S1).

The acute tolerator experienced a range of final mortalities within categories of MHWs, with extreme MHWs (four times above the 90th percentile) causing mortality ranging from 0% to 68.7% (Figure S2, left panel). The chronic tolerator experienced less variation in mortality within MHW categories, and comparatively experienced lower rates of mortality within more intense MHW categories than the acute tolerator categories (extreme MHW mortality range 0%–37%) (Figure S2, centre panel). Finally, the mixed-strategy species experienced the highest level of mortality under the most extreme magnitude and duration MHWs, ranging 0%–96.9% (Figure S2, right panel). All species experienced mortality outside of Hobday categorized MHWs (maximum acute mortality = 13.5%, chronic mortality = 6.1% and mixed-strategy mortality = 28.8%), mostly over MHWs shorter than 5 days.

By design, changing interannual variation did not impact the survival heatmap for the acute tolerator species examined. This

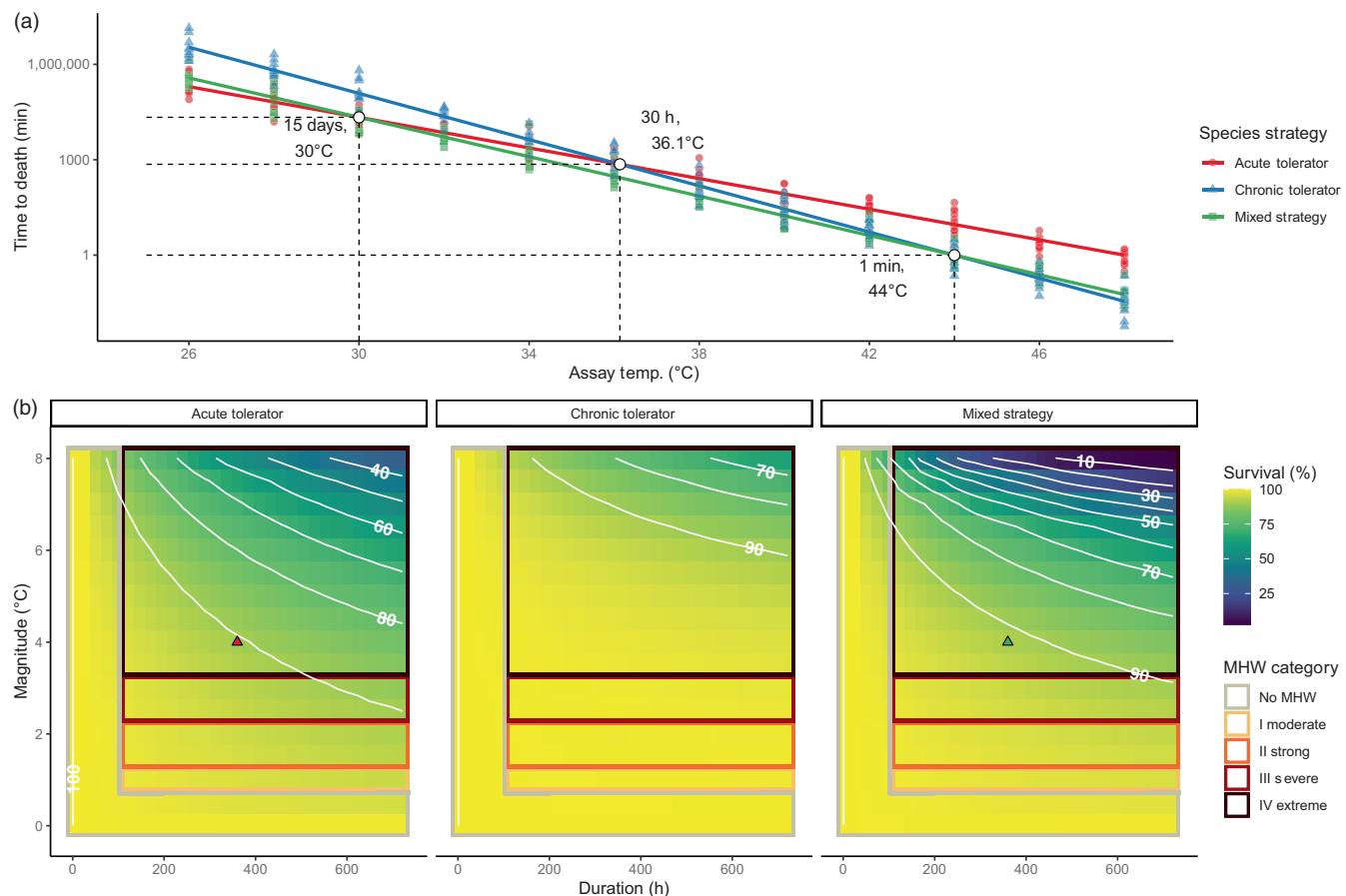


FIGURE 2 (a) Thermal death time curves for three hypothetical species that follow divergent adaptation strategies. One species exhibits an acute tolerator strategy ($CT_{max}=48^{\circ}\text{C}$, $z=4.15$, red circles), one species a chronic tolerator strategy (44°C , 2.75, blue triangles), and one species a mixed strategy (44°C , 3.22°C , green squares). High acute tolerance trades off with a faster time to death with lower exposure temperatures. The intercept of each TDT curve (white points) represents the time and temperature combination at which each species pair exhibits the same survival. (b) Survival varies with magnitude and duration between three species and crosses over fixed-baseline marine heatwave (MHW) categories. Border colour indicates the category of MHW, and heatmap colour the final survival prediction from each MHW. White isolines connect MHW magnitude-duration combinations on the heatmap that resulted in equal survival. The L-shaped grey region contains magnitude-duration combinations that are either not Hobday-defined MHWs (below 90% threshold) and/or are marine heat spikes (<5 days). Note that baseline for MHWs is 26°C . The triangles on the acute tolerator and mixed strategy panels indicate the coordinates of TDT curve intersection between the two species (15 days, 30°C ; see Figure S1 for extended magnitude intersection points).

manipulation altered only the climatological history and thus where Hobday's 90% threshold is calculated, not the MHW profiles themselves. (Figure 3). Decreasing interannual variation increased the number of MHW profiles that were categorized under more extreme categories (Figure 3, +0.25°C), while increasing variation decreased the number of MHW scenarios classified as severe or extreme (Figure 3, +1.5°C). In low variation scenarios, the magnitude between MHW category thresholds were smaller than the magnitude steps in our simulations, and so no simulations were categorized as Moderate or Severe (Figure S3, +0.25°C). With increased annual variation (+1.5°C), low mortality MHWs were less likely to be categorized as severe or extreme (Figure S3).

Maximum mortality for the acute tolerator across all MHW simulations of magnitude was reached at the seasonal maxima (centred August 17, Figure 4, Figure S4). Survival increased following the sinusoidal function composing the annual time series for a given magnitude, with no mortality occurring after 70 days over even the highest magnitude MHWs.

4 | DISCUSSION

For the first time to our knowledge, we compared assessments of MHW strength using thermal tolerance landscapes and dynamic tolerance models (Rezende et al., 2020) and classifications of MHWs using statistical analysis of climatology (Hobday et al., 2016) across a suite of simulated MHWs of varying magnitude and duration. As predicted, we found that a climatological approach to quantifying MHW strength (Hobday et al., 2018) can dramatically misclassify organismal effects, particularly over the strongest MHW categorizations. Further, strictly adhering to a 5-day minimum threshold for classifying MHWs omits the potential for lethal effects during shorter 'heat spike' events. We attribute these mismatches between methods to the reliance on MHW magnitude, rather than the interaction between duration and magnitude, in the fixed-baseline statistical definition. We demonstrated that TDT curve shape and MHW seasonality can yield diverging survival estimates over MHWs within the same statistical category. Further, a climatological

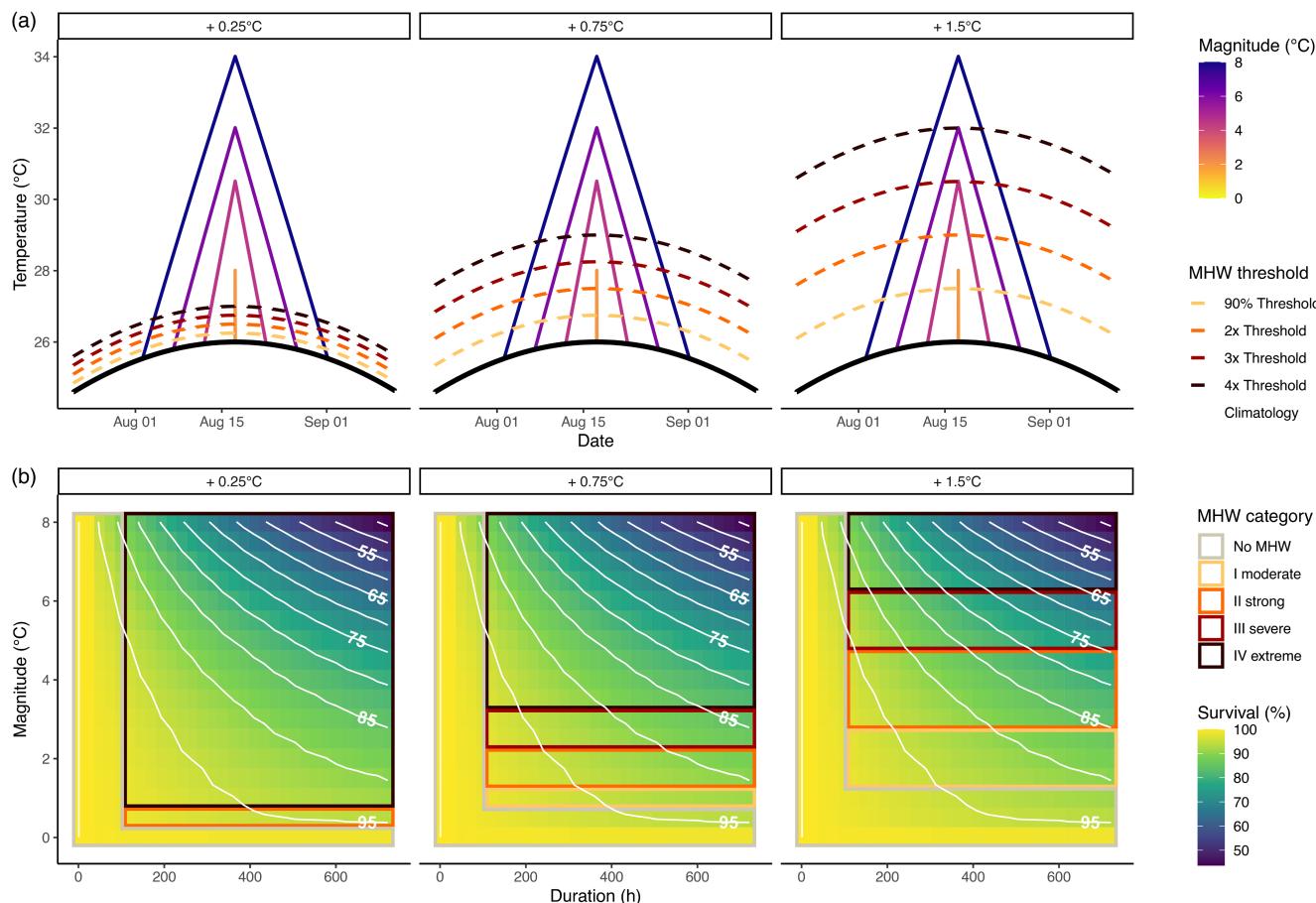
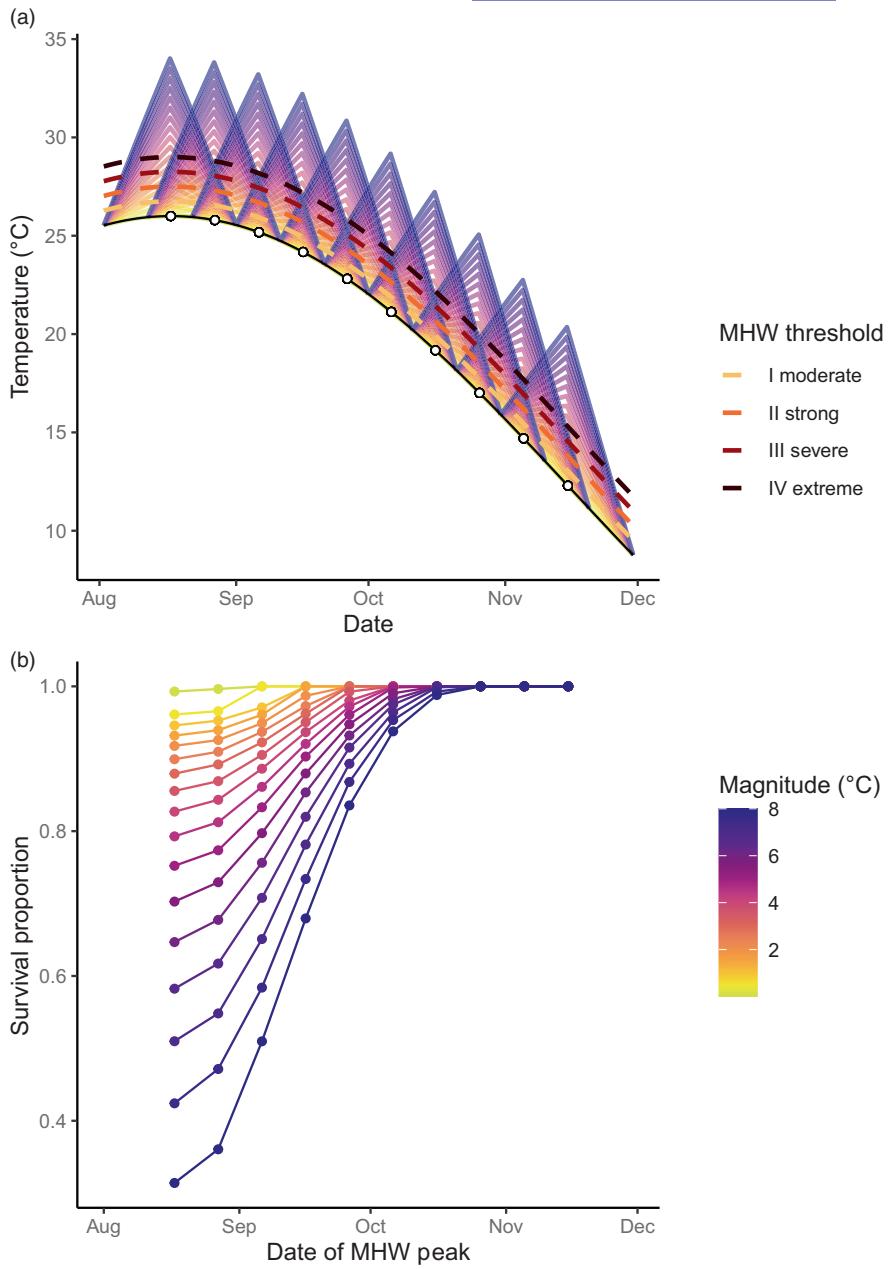


FIGURE 3 (a) Conceptual diagram of how marine heatwave (MHW) categories were manipulated by increasing the interannual variation around mean climatology, thus increasing the 90th percentile by 0.25, 0.75, and 1.5°C. Coloured triangles are four example MHW profiles with different magnitudes—527 were analysed for each variation manipulation. (B) Heatmap of survival predictions for the acute tolerator exposed to simulated MHWs that occur in three distinct varying environments. Panel labels indicate the degrees above climatology at which the 90% threshold starts. Border line colour indicates the category of MHW and heatmap colour, the final survival prediction from each MHW. White isolines connect MHW magnitude-duration combinations with equal survival. The L-shaped grey region contains magnitude-duration combinations that are either not Hobday-defined MHWs (below 90% threshold) and/or are marine heat spikes (<5 days). The middle panel (+0.75°C) is the same as the middle panels in Figure 2. Note that baseline for MHWs is 26°C.

FIGURE 4 (a) Marine heatwaves (MHWs) of fixed duration (24 days) but variable magnitude (0–8°C) were simulated across ten time points post annual maximum (white points, time of maximum exposure). Each MHW was simulated onto the climatological curve (baseline temperature, black line) in isolation for the analysis, but here are displayed stacked for visual purposes. (b) Resulting end of MHW survival for the acute tolerator exposed to each MHW across magnitude-seasonal occurrences.



approach is sensitive to historical climatological variability and can over- or under-predict biological impacts.

In our MHW simulations, mortality tended to be low in the least severe categories, but the range of survival broadened in more severe categories. In some cases, no mortality was predicted to occur in the most statistically extreme MHWs (shorter duration events). In other cases, mortality occurred in non-MHW temperature profiles, particularly during high-magnitude events shorter than 5 days that are otherwise ignored as statistically defined MHWs. By connecting MHW scenarios with equal survival, we show that MHWs with different profiles can have similar biological effects (as indicated along survival isoclines). For example, the acute tolerator experienced similar survival (92%) when a 7.5°C event lasted 3 days and when a 4.5°C

event lasted 10 days. In this example, the 3-day event is classified as a heat spike by the Hobday definition despite having the same effect as an 'extreme' heatwave lasting 10 days. Survival over chronic events tends to be driven proportionally by the magnitude of the event, while survival during acute events is more proportionally governed by the duration of the event. While this may seem to support the approach of categorizing MHW impacts based on magnitude in isolation (especially for events longer than 5 days), short-duration events are common in comparison to long-duration events (Bates et al., 2018; McClanahan, 2022; Pietri et al., 2021). The sensitivity of survival to even low durations further indicate the importance of studying acute heating events with parameters such as tidal and daylight cycles, which are neglected using magnitude-only metrics.

4.1 | TDT curve variation and MHWs

Our analysis demonstrated that a putatively tolerant species when based on a single-tolerance measure (e.g. CT_{max} in isolation) actually experiences higher mortality across virtually all MHW scenarios tested (Figure 2b). The acute tolerator (high CT_{max} , high z) would normally be considered a more tolerant species than the chronic tolerator (low CT_{max} , low z) and mixed-strategy species (low CT_{max} , mid z) due to its higher acute thermal limit. However, because the TDT models for acute and chronic species intersect and diverge relatively quickly (30h, 36.1°C Figure 2a), the chronic tolerator is a more tolerant species over lower temperature magnitudes, regardless of duration (Figure S1). The acute species outperforms the mixed strategy species, but only at exposures above their TDT curve intersection (beyond 15 days and 30°C, Figure 2a). Thus, relying on CT_{max} or z in isolation will therefore result in inaccurate relative ranking of species tolerance, an implication that is only made clear through the application of thermal tolerance landscapes and dynamic tolerance models.

Given species with intersecting TDT curves can be part of the same local species assemblages, such as with marine bivalves and freshwater fish (Bertolini et al., 2023; Troia, 2023), the scaling factor z likely plays a more significant role in comparing species and population sensitivities than CT_{max} when considering non-acute MHW events (Rezende et al., 2014). The drivers behind adaptation in CT_{max} /z are unstudied across taxa, providing an opportunity to further understand the links between this parameter set and the evolution of thermal strategies. We demonstrated that variation in these parameters has a significant role on organismal tolerance to MHWs, and different adaptive strategies will result in differential organismal outcomes to a shared MHW.

4.2 | Interannual variation and MHW categorization

By design, manipulating interannual seasonal variation but holding species adaptive strategy (the CT_{max} and z parameters) constant did not have an impact on organism survival. Instead, changes to climatological variation influences how the 90th percentile of climatology is calculated, and in turn how categories are assigned to MHWs (Hobday et al., 2018). Increasing annual variation tended to mask events with lethal risk by downgrading their categorization. Decreasing variation had the opposite effect of upgrading MHW categorization, lumping MHWs with low and high survival together in extreme categories. An expected organismal response to variable environments is the evolution of plasticity in thermal tolerance, which can change the shape of TDT curves in response to changes in acclimation conditions (Castañeda et al., 2015; Semsar-kazerouni & Verberk, 2018; Verberk et al., 2023). Our analysis does not change TDT shape through the year and thus does not account for evolved plasticity and acclimation effects in response to environmental variation.

4.3 | Seasonal timing of MHWs

We found that mortality across all MHW simulations decreased with distance from the summer maximum, following the shape of the underlying sine wave describing seasonal temperature variation. Despite mortality essentially approaching zero by mid-October, the severity of MHWs as classified using a climatological approach remained the same. Since the timing of extreme events against the backdrop of the environment is an important modulator of how organisms experience and react to these events, the Hobday MHW framework may overestimate lethal biological effects outside of annual extremes (Cinto Mejía & Wetzel, 2023; Ern et al., 2023). MHW timing can influence organism responses by their occurrence against cyclic environmental factors (e.g. seasons and tides) as well as against organism phenology and biological clocks (e.g. spawning and development; Bernhardt et al., 2020; Giménez, 2023). Organisms are more likely to experience sublethal effects from MHWs that do not occur over seasonal maxima, but which may impact population and community structure just as strongly as lethal effects (Jentsch et al., 2007). Additionally, acclimation is likely to play a critical role in determining whether an off-peak MHW is stressful, based on deviations of the MHW from preceding conditions (Dowd & Denny, 2020). Flattening of annual temperature cycles and the elongation of summers (Wang & Dillon, 2014; Wang et al., 2021) may reduce the seasonal timing refugia from off-peak MHWs and enlarge risky periods of stress for organisms. Properly selected TDT curves will replicate how an organism experiences and reacts to timing of their thermal environment (e.g. through acclimation, life stage, and behaviour) should overcome the sources of variation outlined above.

4.4 | Limitations and future directions

As with any modelling framework, applying dynamic thermal tolerance models to classifying MHWs has limitations. Thermal tolerance can vary across many contexts and organism states, including acclimation (Castañeda et al., 2015; Semsar-kazerouni & Verberk, 2018; Verberk et al., 2023), developmental plasticity (Pottier et al., 2022), life stage and size (Cinto Mejía & Wetzel, 2023; Dahlke et al., 2020; Peralta-Maraver & Rezende, 2021; Truebano et al., 2018), intraspecific (Dwane et al., 2021) and interspecific (Rezende et al., 2014) variation, seasonal timing (Ern et al., 2023), metabolic state (Guppy & Withers, 1999; Semsar-kazerouni et al., 2020; Vajedsamiei et al., 2021) and oxygen availability (Pörtner, 2010; Verberk et al., 2016). In particular, we highlight that acclimation will likely play an outsized role in determining the shape of TDT curves. Previous work on *Drosophila* found warm acclimation to increase CT_{max} while increasing z (chronic tolerance; Castañeda et al., 2015), while in amphipods warm acclimation actually decreased or caused little change in z (Semsar-kazerouni & Verberk, 2018; Verberk et al., 2023). Additionally, there remains open questions as to whether organisms acclimate to the mean

or maximum conditions and how the length and variability of a pre-MHW acclimation window impact ultimate survival (Dowd & Denny, 2020).

We also assume mortality from a MHW event is directly attributable to temperature stress. Mortality may also occur due to multiple biotic and abiotic stressors co-occurring with temperature (Buckley & Kingsolver, 2021; Dowd et al., 2015; Ern et al., 2023; Litchman & Thomas, 2023). Even with perfectly chosen TDT curves, behavioural thermoregulation is likely to play a significant role in mediating organism mortality to MHWs (Chapperon & Seuront, 2011; Kearney et al., 2009). Even relatively nonmobile organisms like clams can change their thermal exposure by burrowing deeper into cooler sediment (Domínguez et al., 2021; Macho et al., 2016). Mismatches between predictions and observations mortality are therefore likely, but predictions of mortality from a single driver can serve as a null model over which stress synergies and covariance effects can be observed (Gerhard et al., 2023; Litchman & Thomas, 2023).

In our MHW simulations, we did not include two additional parameters that are likely to mediate organism responses: rate of onset and frequency/return time (Hobday et al., 2016). MHW rate of onset, or ramping rate, is itself a function of magnitude-duration of temperature, and thus has an impact on stress accumulation within an organism (Kingsolver & Umpanhowar, 2018; Rezende et al., 2011, 2020). Further, we did not investigate event frequency (return time) of MHWs because dynamic tolerance models do not currently allow for incomplete organism recovery between MHW events (Jørgensen et al., 2021; Ørsted et al., 2022; Seuront et al., 2019), although analyses considering full or no recovery are possible. Future work could examine the theoretical underpinnings of post-event recovery, as this will likely have a non-linear effect on mortality (Seuront et al., 2019; Stein et al., 2023).

Conducting experimental assays to obtain TDT data for organisms is time and resource consuming, and it will likely be impossible to account for all possible TDT curves for a given species across life stage, acclimation, population, size and other traits without killing large groups of focal organisms. Researchers and managers should consider their goal of assessing MHW strength and consider an alternative approach that considers organismal physiology if ecosystem and organism impacts are the main interest by selecting sentinel and/or model species when possible under a TDT approach. With these limitations in mind, the Hobday approach to categorizing MHWs requires less parameterization, and remains an important tool for rapidly assessing the potential for ecosystem effects of MHWs.

Finally, empirical evidence is needed to support the model results in this analysis. Exposing organisms to laboratory MHWs and comparing measured mortality with modelled mortality will help clarify the applicability of dynamic tolerance models across taxa and MHW profiles. Within our results, we identified survival isolines that connect MHW profiles with equal survival. Testing these profiles experimentally and observing where divergences from this expectation occur will help identify any departures from the TDT framework, and ultimately its limitations. Bayesian approaches may

close this predictive gap by directly parameterizing thermal tolerance landscapes from field data (Vajedsamiei et al., 2024). Continued work integrating dynamic tolerance models into population, species interaction, and ecosystem models will strengthen the mechanistic basis behind forecasts of MHW impacts.

5 | CONCLUSIONS

Building a mechanistic understanding of the physiological effects of MHWs can allow for predictions of MHW effects across scales of ecological organization (Twiname et al., 2020). As MHWs become more predictable (Jacox et al., 2022), forecasting of ecological impacts across scale using workflows like the dynamic tolerance models presented here will become more feasible, thereby helping predict MMEs, population collapse and species extinction events (Cerini et al., 2023; Verberk et al., 2023). Developing predictive warning systems that can predict ecological climate can give individuals, communities, managers and governments context-specific information and actionable avoidance, mitigation or adaptation options.

AUTHOR CONTRIBUTIONS

Andrew R. Villeneuve and Easton R. White were both involved in research conceptualization, funding acquisition and manuscript editing. Andrew R. Villeneuve developed the methodology, analysed the data and wrote the original manuscript. All authors contributed to the draft and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.8w9ghx3tx> (Villeneuve & White, 2024).

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REFERENCES

Ansell, A. D., Barnett, P. R. O., Bodoy, A., & Massé, H. (1980). Upper temperature tolerances of some European molluscs II. *Donax vittatus*, D.

- semistriatus* and *D. trunculus*. *Marine Biology*, 58(1), 41–46. <https://doi.org/10.1007/BF00386878>
- Ansell, A. D., Barnett, P. R. O., Bodoy, A., & Massé, H. (1981). Upper temperature tolerances of some European molluscs: III. *Cardium glaucum*, *C. tuberculatum* and *C. edule*. *Marine Biology*, 65(2), 177–183. <https://doi.org/10.1007/BF00397083>
- Bailey, L. D., & van de Pol, M. (2016). Tackling extremes: Challenges for ecological and evolutionary research on extreme climatic events. *Journal of Animal Ecology*, 85(1), 85–96. <https://doi.org/10.1111/1365-2656.12451>
- Bates, A. E., Helmuth, B., Burrows, M. T., Duncan, M. I., Garrabou, J., Guy-Haim, T., Lima, F., Queiros, A. M., Seabra, R., Marsh, R., Belmaker, J., Bensoussan, N., Dong, Y., Mazaris, A. D., Smale, D., Wahl, M., & Rilov, G. (2018). Biologists ignore ocean weather at their peril. *Nature*, 560(7718), 299–301. <https://doi.org/10.1038/d41586-018-05849-5>
- Bernhardt, J. R., O'Connor, M. I., Sunday, J. M., & Gonzalez, A. (2020). Life in fluctuating environments. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 375(1814), 20190454. <https://doi.org/10.1098/rstb.2019.0454>
- Bertolini, C., Glaser, D., Canu, M., & Pastres, R. (2023). Coupling habitat-specific temperature scenarios with tolerance landscape to predict the impacts of climate change on farmed bivalves. *Marine Environmental Research*, 188, 106038. <https://doi.org/10.1016/j.marenvres.2023.106038>
- 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. <https://doi.org/10.1016/j.ecss.2021.107284>
- Buckley, L. B., & Kingsolver, J. G. (2021). Evolution of thermal sensitivity in changing and variable climates. *Annual Review of Ecology, Evolution, and Systematics*, 52(1), 563–586. <https://doi.org/10.1146/annurev-ecolsys-011521-102856>
- Carter, M. J., García-Huidobro, M. R., Aldana, M., Rezende, E. L., Bozinovic, F., Galbán-Malagón, C., & Pulgar, J. M. (2023). Upper thermal limits and risk of mortality of coastal Antarctic ectotherms. *Frontiers in Marine Science*, 9, 1108330. <https://doi.org/10.3389/fmars.2022.1108330>
- Castañeda, L. E., Rezende, E. L., & Santos, M. (2015). Heat tolerance in *Drosophila subobscura* along a latitudinal gradient: Contrasting patterns between plastic and genetic responses. *Evolution*, 69(10), 2721–2734. <https://doi.org/10.1111/evo.12757>
- Cerini, F., Childs, D. Z., & Clements, C. F. (2023). A predictive timeline of wildlife population collapse. *Nature Ecology & Evolution*, 7(3), Article 3. <https://doi.org/10.1038/s41559-023-01985-2>
- Chapperon, C., & Seuront, L. (2011). Behavioral thermoregulation in a tropical gastropod: Links to climate change scenarios. *Global Change Biology*, 17(4), 1740–1749. <https://doi.org/10.1111/j.1365-2486.2010.02356.x>
- Cinto Mejía, E., & Wetzel, W. C. (2023). The ecological consequences of the timing of extreme climate events. *Ecology and Evolution*, 13(1), e9661. <https://doi.org/10.1002/ece3.9661>
- Dahlke, F. T., Wohlrab, S., Butzin, M., & Pörtner, H.-O. (2020). Thermal bottlenecks in the life cycle define climate vulnerability of fish. *Science*, 369(6499), 65–70. <https://doi.org/10.1126/science.aaz3658>
- Davis, K. A., Lentz, S. J., Pineda, J., Farrar, J. T., Starczak, V. R., & Churchill, J. H. (2011). Observations of the thermal environment on Red Sea platform reefs: A heat budget analysis. *Coral Reefs*, 30(1), 25–36. <https://doi.org/10.1007/s00338-011-0740-8>
- Denny, M. W., & Paine, R. T. (1998). Celestial mechanics, sea-level changes, and intertidal ecology. *The Biological Bulletin*, 194(2), 108–115. <https://doi.org/10.2307/1543040>
- Domínguez, R., Olabarria, C., Woodin, S. A., Wethey, D. S., Peteiro, L. G., Macho, G., & Vázquez, E. (2021). Contrasting responsiveness of four ecologically and economically important bivalves to simulated heat waves. *Marine Environmental Research*, 164, 105229. <https://doi.org/10.1016/j.marenvres.2020.105229>
- Dong, Y.-W. (2023). Roles of multi-level temperature-adaptive responses and microhabitat variation in establishing distributions of intertidal species. *Journal of Experimental Biology*, 226(21), jeb245745. <https://doi.org/10.1242/jeb.245745>
- Dowd, W. W., & Denny, M. W. (2020). A series of unfortunate events: Characterizing the contingent nature of physiological extremes using long-term environmental records. *Proceedings of the Royal Society B: Biological Sciences*, 287(1918), 1–9. <https://www.jstor.org/stable/26917346>
- Dowd, W. W., King, F. A., & Denny, M. W. (2015). Thermal variation, thermal extremes and the physiological performance of individuals. *Journal of Experimental Biology*, 218(12), 1956–1967. <https://doi.org/10.1242/jeb.114926>
- Dwane, C., Rundle, S. D., Tills, O., Rezende, E. L., Galindo, J., Rolán-Alvarez, E., & Truebano, M. (2021). Divergence in thermal physiology could contribute to vertical segregation in intertidal ecotypes of *Littorina saxatilis*. *Physiological and Biochemical Zoology: PBZ*, 94(6), 353–365. <https://doi.org/10.1086/716176>
- Ern, R., Andreassen, A. H., & Jutfelt, F. (2023). Physiological mechanisms of acute upper thermal tolerance in fish. *Physiology*, 38, 141–158. <https://doi.org/10.1152/physiol.00027.2022>
- Fey, S. B., Siepielski, A. M., Nusslé, S., Cervantes-Yoshida, K., Hwan, J. L., Huber, E. R., Fey, M. J., Catenazzi, A., & Carlson, S. M. (2015). Recent shifts in the occurrence, cause, and magnitude of animal mass mortality events. *Proceedings of the National Academy of Sciences of the United States of America*, 112(4), 1083–1088. <https://doi.org/10.1073/pnas.1414894112>
- Frölicher, T. L., Fischer, E. M., & Gruber, N. (2018). Marine heatwaves under global warming. *Nature*, 560(7718), 360–364. <https://doi.org/10.1038/s41586-018-0383-9>
- Garrabou, J., Gómez-Gras, D., Medrano, A., Cerrano, C., Ponti, M., Schlegel, R., Bensoussan, N., Turicchia, E., Sini, M., Gerovasileiou, V., Teixido, N., Mirasole, A., Tamburello, L., Cebrian, E., Rilov, G., Ledoux, J., Souissi, J. B., Khamassi, F., Ghanem, R., ... Harmelin, J. (2022). Marine heatwaves drive recurrent mass mortalities in the Mediterranean Sea. *Global Change Biology*, 28(19), 5708–5725. <https://doi.org/10.1111/gcb.16301>
- Gerhard, M., Koussoroplis, A.-M., Raatz, M., Pansch, C., Fey, S. B., Vajedsamie, J., Calderó-Pascual, M., Cunillera-Montcusí, D., Juvigny-Khenafou, N. P. D., Polazzo, F., Thomas, P. K., Symons, C. C., Beklioğlu, M., Berger, S. A., Chefaoui, R. M., Ger, K. A., Langenheder, S., Nejstgaard, J. C., Ptacník, R., & Striebel, M. (2023). Environmental variability in aquatic ecosystems: Avenues for future multifactorial experiments. *Limnology and Oceanography Letters*, 8(2), 247–266. <https://doi.org/10.1002/lol2.10286>
- Giménez, L. (2023). A geometric approach to understanding biological responses to environmental fluctuations from the perspective of marine organisms. *Marine Ecology Progress Series*, 721, 17–38. <https://doi.org/10.3354/meps14414>
- Glynn, P. W. (1968). Mass mortalities of echinoids and other reef flat organisms coincident with midday, low water exposures in Puerto Rico. *Marine Biology*, 1(3), 226–243. <https://doi.org/10.1007/BF00347116>
- González-Trujillo, J. D., Román-Cuesta, R. M., Muñiz-Castillo, A. I., Amaral, C. H., & Araújo, M. B. (2023). Multiple dimensions of extreme weather events and their impacts on biodiversity. *Climatic Change*, 176(11), 155. <https://doi.org/10.1007/s10584-023-03622-0>
- Guppy, M., & Withers, P. (1999). Metabolic depression in animals: Physiological perspectives and biochemical generalizations.

- Biological Reviews*, 74(1), 1–40. <https://doi.org/10.1017/S0006323198005258>
- Harris, R. M. B., Beaumont, L. J., Vance, T. R., Tozer, C. R., Remenyi, T. A., Perkins-Kirkpatrick, S. E., Mitchell, P. J., Nicotra, A. B., McGregor, S., Andrew, N. R., Letnic, M., Kearney, M. R., Wernberg, T., Hutley, L. B., Chambers, L. E., Fletcher, M.-S., Keatley, M. R., Woodward, C. A., Williamson, G., ... Bowman, D. M. J. S. (2018). Biological responses to the press and pulse of climate trends and extreme events. *Nature. Climate Change*, 8(7), Article 7. <https://doi.org/10.1038/s41558-018-0187-9>
- Harvey, B. P., Marshall, K. E., Harley, C. D. G., & Russell, B. D. (2022). Predicting responses to marine heatwaves using functional traits. *Trends in Ecology & Evolution*, 37(1), 20–29. <https://doi.org/10.1016/j.tree.2021.09.003>
- Helmuth, B. S. (2009). From cells to coastlines: How can we use physiology to forecast the impacts of climate change? *Journal of Experimental Biology*, 212(6), 753–760. <https://doi.org/10.1242/jeb.023861>
- Helmuth, B. S., Broitman, B. R., Blanchette, C. A., Gilman, S., Halpin, P., Harley, C. D. G., O'Donnell, M. J., Hofmann, G. E., Menge, B., & Strickland, D. (2006). Mosaic patterns of thermal stress in the rocky intertidal zone: Implications for climate change. *Ecological Monographs*, 76(4), 461–479. [https://doi.org/10.1890/0012-9615\(2006\)076\[0461:MPOTSI\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2006)076[0461:MPOTSI]2.0.CO;2)
- Heron, S., Johnston, L., Liu, G., Geiger, E., Maynard, J., De La Cour, J., Johnson, S., Okano, R., Benavente, D., Burgess, T., Iguel, J., Perez, D., Skirving, W., Strong, A., Tirak, K., & Eakin, C. (2016). Validation of reef-scale thermal stress satellite products for coral bleaching monitoring. *Remote Sensing*, 8(1), 59. <https://doi.org/10.3390/rs8010059>
- 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. <https://doi.org/10.1016/j.pocean.2015.12.014>
- Hobday, A. J., Oliver, E., Sen Gupta, A., Benthuysen, J., Burrows, M., Donat, M., Holbrook, N., Moore, P., Thomsen, M., Wernberg, T., & Smale, D. (2018). Categorizing and naming marine heatwaves. *Oceanography*, 31(2), 162–173. <https://doi.org/10.5670/oceanog.2018.205>
- 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), Article 1. <https://doi.org/10.1038/s41467-019-10206-z>
- Jacox, M. G., Alexander, M. A., Amaya, D., Becker, E., Bograd, S. J., Brodie, S., Hazen, E. L., Pozo Buil, M., & Tommasi, D. (2022). Global seasonal forecasts of marine heatwaves. *Nature*, 604(7906), Article 7906. <https://doi.org/10.1038/s41586-022-04573-9>
- Jentsch, A., Kreyling, J., & Beierkuhnlein, C. (2007). A new generation of climate-change experiments: Events, not trends. *Frontiers in Ecology and the Environment*, 5(7), 365–374. [https://doi.org/10.1890/1540-9295\(2007\)5\[365:ANGOCE\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2007)5[365:ANGOCE]2.0.CO;2)
- 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. <https://doi.org/10.1038/s41598-021-92004-6>
- Jurgens, L. J., Rogers-Bennett, L., Raimondi, P. T., Schiebelhut, L. M., Dawson, M. N., Grosberg, R. K., & Gaylord, B. (2015). Patterns of mass mortality among rocky shore invertebrates across 100 km of northeastern Pacific coastline. *PLoS One*, 10(6), e0126280. <https://doi.org/10.1371/journal.pone.0126280>
- Kearney, M., Shine, R., & Porter, W. P. (2009). The potential for behavioral thermoregulation to buffer “cold-blooded” animals against climate warming. *Proceedings of the National Academy of Sciences of the United States of America*, 106(10), 3835–3840. <https://doi.org/10.1073/pnas.0808913106>
- Kingsolver, J. G., & Umpanhowar, J. (2018). The analysis and interpretation of critical temperatures. *Journal of Experimental Biology*, 221(12), jeb167858. <https://doi.org/10.1242/jeb.167858>
- Litchman, E., & Thomas, M. K. (2023). Are we underestimating the ecological and evolutionary effects of warming? Interactions with other environmental drivers may increase species vulnerability to high temperatures. *Oikos*, 2023(2), e09155. <https://doi.org/10.1111/oik.09155>
- Macho, G., Woodin, S. A., Wethey, D. S., & Vázquez, E. (2016). Impacts of sublethal and lethal high temperatures on clams exploited in European fisheries. *Journal of Shellfish Research*, 35(2), 405–419. <https://doi.org/10.2983/035.035.0215>
- McClanahan, T. R. (2022). Coral responses to climate change exposure. *Environmental Research Letters*, 17(7), 073001. <https://doi.org/10.1088/1748-9326/ac7478>
- Molina, A. N., Pulgar, J. M., Rezende, E. L., & Carter, M. J. (2022). Heat tolerance of marine ectotherms in a warming Antarctica. *Global Change Biology*, 29(1), 179–188. <https://doi.org/10.1111/gcb.16402>
- Morash, A. J., Neufeld, C., MacCormack, T. J., & Currie, S. (2018). The importance of incorporating natural thermal variation when evaluating physiological performance in wild species. *Journal of Experimental Biology*, 221(14), jeb164673. <https://doi.org/10.1242/jeb.164673>
- Neuner, G., & Buchner, O. (2023). The dose makes the poison: The longer the heat lasts, the lower the temperature for functional impairment and damage. *Environmental and Experimental Botany*, 212, 105395. <https://doi.org/10.1016/j.envexpbot.2023.105395>
- Oliver, E. C. J., Benthuysen, J. A., Darmaraki, S., Donat, M. G., Hobday, A. J., Holbrook, N. J., Schlegel, R. W., & Sen Gupta, A. (2021). Marine heatwaves. *Annual Review of Marine Science*, 13(1), 313–342. <https://doi.org/10.1146/annurev-marine-032720-095144>
- Ørsted, M., Jørgensen, L. B., & Overgaard, J. (2022). Finding the right thermal limit: A framework to reconcile ecological, physiological and methodological aspects of CTmax in ectotherms. *Journal of Experimental Biology*, 225(19), jeb244514. <https://doi.org/10.1242/jeb.244514>
- Pansch, C., Scotti, M., Barboza, F. R., Al-Janabi, B., Brakel, J., Briski, E., Buchholz, B., Franz, M., Ito, M., Paiva, F., Saha, M., Sawall, Y., Weinberger, F., & Wahl, M. (2018). Heat waves and their significance for a temperate benthic community: A near-natural experimental approach. *Global Change Biology*, 24(9), 4357–4367. <https://doi.org/10.1111/gcb.14282>
- Peralta-Maraver, I., & Rezende, E. L. (2021). Heat tolerance in ectotherms scales predictably with body size. *Nature Climate Change*, 11(1), Article 1. <https://doi.org/10.1038/s41558-020-00938-y>
- Pietri, A., Colas, F., Mogollon, R., Tam, J., & Gutierrez, D. (2021). Marine heatwaves in the Humboldt current system: From 5-day localized warming to year-long El Niños. *Scientific Reports*, 11, 21172. <https://doi.org/10.1038/s41598-021-00340-4>
- Pörtner, H.-O. (2010). Oxygen- and capacity-limitation of thermal tolerance: A matrix for integrating climate-related stressor effects in marine ecosystems. *Journal of Experimental Biology*, 213(6), 881–893. <https://doi.org/10.1242/jeb.037523>
- Pottier, P., Burke, S., Zhang, R. Y., Noble, D. W. A., Schwanz, L. E., Drobniak, S. M., & Nakagawa, S. (2022). Developmental plasticity in thermal tolerance: Ontogenetic variation, persistence, and future directions. *Ecology Letters*, 25(10), 2245–2268. <https://doi.org/10.1111/ele.14083>
- Raymond, W. W., Barber, J. S., Dethier, M. N., Hayford, H. A., Harley, C. D. G., King, T. L., Paul, B., Speck, C. A., Tobin, E. D., Raymond, A. E. T., & McDonald, P. S. (2022). Assessment of the impacts of an

- unprecedented heatwave on intertidal shellfish of the Salish Sea. *Ecology*, 103(10), e3798. <https://doi.org/10.1002/ecy.3798>
- Reid, E. C., Lentz, S. J., DeCarlo, T. M., Cohen, A. L., & Davis, K. A. (2020). Physical processes determine spatial structure in water temperature and residence time on a wide reef flat. *Journal of Geophysical Research: Oceans*, 125(12), e2020JC016543. <https://doi.org/10.1029/2020JC016543>
- Rezende, E. L., Bozinovic, F., Szilágyi, A., & Santos, M. (2020). Predicting temperature mortality and selection in natural *Drosophila* populations. *Science*, 369(6508), 1242–1245. <https://doi.org/10.1126/science.aba9287>
- Rezende, E. L., Castañeda, L. E., & Santos, M. (2014). Tolerance landscapes in thermal ecology. *Functional Ecology*, 28(4), 799–809. <https://doi.org/10.1111/1365-2435.12268>
- Rezende, E. L., Tejedo, M., & Santos, M. (2011). Estimating the adaptive potential of critical thermal limits: Methodological problems and evolutionary implications. *Functional Ecology*, 25(1), 111–121. <https://doi.org/10.1111/j.1365-2435.2010.01778.x>
- Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., & Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature*, 413(6856), 591–596. <https://doi.org/10.1038/35098000>
- Schlegel, R. W., & Smit, A. J. (2018). heatwaveR: A central algorithm for the detection of heatwaves and cold-spells. *Journal of Open Source Software*, 3(27), 821. <https://doi.org/10.21105/joss.00821>
- Semsar-kazerouni, M., Boerrigter, J. G. J., & Verberk, W. C. E. P. (2020). Changes in heat stress tolerance in a freshwater amphipod following starvation: The role of oxygen availability, metabolic rate, heat shock proteins and energy reserves. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 245, 110697. <https://doi.org/10.1016/j.cbpa.2020.110697>
- Semsar-kazerouni, M., & Verberk, W. C. E. P. (2018). It's about time: Linkages between heat tolerance, thermal acclimation and metabolic rate at different temporal scales in the freshwater amphipod *Gammarus fossarum* Koch, 1836. *Journal of Thermal Biology*, 75, 31–37. <https://doi.org/10.1016/j.jtherbio.2018.04.016>
- Seuront, L., Nicastro, K. R., Zardi, G. I., & Goerville, E. (2019). Decreased thermal tolerance under recurrent heat stress conditions explains summer mass mortality of the blue mussel *Mytilus edulis*. *Scientific Reports*, 9(1), Article 1. <https://doi.org/10.1038/s41598-019-53580-w>
- Skirving, W., Marsh, B., De La Cour, J., Liu, G., Harris, A., Maturi, E., Geiger, E., & Eakin, C. M. (2020). CoralTemp and the coral reef watch coral bleaching heat stress product suite version 3.1. *Remote Sensing*, 12(23), 3856. <https://doi.org/10.3390/rs12233856>
- Slein, M. A., Bernhardt, J. R., O'Connor, M. I., & Fey, S. B. (2023). Effects of thermal fluctuations on biological processes: A meta-analysis of experiments manipulating thermal variability. *Proceedings of the Royal Society B: Biological Sciences*, 290(1992), 20222225. <https://doi.org/10.1098/rspb.2022.2225>
- Smale, D. A., Wernberg, T., Oliver, E. C. J., Thomsen, M., Harvey, B. P., Straub, S. C., Burrows, M. T., Alexander, L. V., Benthuysen, J. A., Donat, M. G., Feng, M., Hobday, A. J., Holbrook, N. J., Perkins-Kirkpatrick, S. E., Scannell, H. A., Sen Gupta, A., Payne, B. L., & Moore, P. J. (2019). Marine heatwaves threaten global biodiversity and the provision of ecosystem services. *Nature Climate Change*, 9(4), 306–312. <https://doi.org/10.1038/s41558-019-0412-1>
- Smith, K. E., Burrows, M. T., Hobday, A. J., King, N. G., Moore, P. J., Sen Gupta, A., Thomsen, M. S., Wernberg, T., & Smale, D. A. (2023). Biological impacts of marine heatwaves. *Annual Review of Marine Science*, 15(1), 119–145. <https://doi.org/10.1146/annurev-marine-032122-121437>
- Ticklebank, K. A., Grace, R. V., & Pilditch, C. A. (2021). Decadal population dynamics of an intertidal bivalve (*Austrovenus stutchburyi*) bed: Pre- and post- a mass mortality event. *New Zealand Journal of Marine and Freshwater Research*, 55(2), 352–374. <https://doi.org/10.1080/00288330.2020.1772323>
- Troia, M. J. (2023). Magnitude-duration relationships of physiological sensitivity and environmental exposure improve climate change vulnerability assessments. *Ecography*, 2023(1), e06217. <https://doi.org/10.1111/ecog.06217>
- Truebano, M., Fenner, P., Tills, O., Rundle, S. D., & Rezende, E. L. (2018). Thermal strategies vary with life history stage. *The Journal of Experimental Biology*, 221(8), jeb171629. <https://doi.org/10.1242/jeb.171629>
- Twiname, S., Audzijonyte, A., Blanchard, J. L., Champion, C., de la Chesnais, T., Fitzgibbon, Q. P., Fogarty, H. E., Hobday, A. J., Kelly, R., Murphy, K. J., Oellermann, M., Peinado, P., Tracey, S., Villanueva, C., Wolfe, B., & Pecl, G. T. (2020). A cross-scale framework to support a mechanistic understanding and modelling of marine climate-driven species redistribution, from individuals to communities. *Ecography*, 43(12), 1764–1778. <https://doi.org/10.1111/ecog.04996>
- Vajedsamie, 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, 660427. <https://doi.org/10.3389/fmars.2021.660427>
- Vajedsamie, J., Warlo, N., Meier, H. E. M., & Melzner, F. (2024). A Bayesian overhaul of thermal tolerance landscape models: Predicting ectotherm lethality buildup and survival amid heatwaves. (p. 2024.01.23.576827). bioRxiv. <https://doi.org/10.1101/2024.01.23.576827>
- van de Pol, M., Jenouvrier, S., Cornelissen, J. H. C., & Visser, M. E. (2017). Behavioural, ecological and evolutionary responses to extreme climatic events: Challenges and directions. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, 372(1723), 20160134. <https://doi.org/10.1098/rstb.2016.0134>
- Verberk, W. C. E. P., Hoefnagel, K. N., Peralta-Maraver, I., Flory, M., & Rezende, E. L. (2023). Long-term forecast of thermal mortality with climate warming in riverine amphipods. *Global Change Biology*, 29(17), 5033–5043. <https://doi.org/10.1111/gcb.16834>
- Verberk, W. C. E. P., Overgaard, J., Ern, R., Bayley, M., Wang, T., Boardman, L., & Terblanche, J. S. (2016). Does oxygen limit thermal tolerance in arthropods? A critical review of current evidence. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 192, 64–78. <https://doi.org/10.1016/j.cbpa.2015.10.020>
- Villeneuve, A. R., & White, E. (2024). Dataset and scripts from: Predicting organismal response to marine heatwaves using dynamic thermal tolerance landscape models. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.8w9ghx3tx>
- Wahl, M., Barboza, F. R., Buchholz, B., Dobretsov, S., Guy-Haim, T., Rilov, G., Schuett, R., Wolf, F., Vajedsamie, J., Yazdanpanah, M., & Pansch, C. (2021). Pulsed pressure: Fluctuating impacts of multifactorial environmental change on a temperate macroalgal community. *Limnology and Oceanography*, 66(12), 4210–4226. <https://doi.org/10.1002/limo.11954>
- Wang, G., & Dillon, M. E. (2014). Recent geographic convergence in diurnal and annual temperature cycling flattens global thermal profiles. *Nature. Climate Change*, 4(11), Article 11. <https://doi.org/10.1038/nclimate2378>
- Wang, J., Guan, Y., Wu, L., Guan, X., Cai, W., Huang, J., Dong, W., & Zhang, B. (2021). Changing lengths of the four seasons by global warming. *Geophysical Research Letters*, 48(6), e2020GL091753. <https://doi.org/10.1029/2020GL091753>
- White, R. H., Anderson, S., Booth, J. F., Braich, G., Draeger, C., Fei, C., Harley, C. D. G., Henderson, S. B., Jakob, M., Lau, C.-A., Mareshet Admasu, L., Narinesingh, V., Rodell, C., Roocroft, E., Weinberger, K. R., & West, G. (2023). The unprecedented Pacific Northwest heatwave of June 2021. *Nature Communications*, 14(1), Article 1. <https://doi.org/10.1038/s41467-023-36289-3>

SUPPORTING INFORMATION

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

Figure S1. Heatmap of survival results over extended magnitude range (0–22°C) across three species, complementary to Figure 2B in the main text.

Figure S2. Proportion of survival predictions, rounded to the nearest 0.05, within each MHW category for three different hypothetical species.

Figure S3. Proportion of survival predictions, rounded to nearest 0.05, within each MHW category for three different variable environments for the acute tolerator species.

Figure S4. Proportion of survival predictions within each MHW category, rounded to nearest 0.05, across eight seasonal occurrences ranging from 0 to 70 days post annual temperature maximum.

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