1 **Predicting organismal response to marine heatwaves using mechanistic thermal**

2 **landscape models**

3 Andrew R. Villeneuve[1]*, Easton R. White[1]

4 [1]Department of Biological Sciences, University of New Hampshire, NH, USA

5 *Corresponding author: drew.villeneuve@unh.edu

6 Acknowledgements

11 Author Contributions

12 ARV and ERW were involved in research conceptualization, funding acquisition, and manuscript editing.

13 ARW developed the methodology, analyzed the data, and wrote the original manuscript. All authors

14 contributed to the draft and gave final approval for publication.

15 Data availability

16 Data and scripts are available from Github: https://github.com/villesci/mhw_simulation_manuscript.

17 ORCID

18 Andrew Villeneuve https://orcid.org/0000-0001-7303-5931

19 Easton White https://orcid.org/0000-0002-0768-9555

Abstract

Marine heatwaves (MHWs) can cause thermal stress in marine ectotherms, experienced as a pulse against the press of anthropogenic warming. When thermal stress exceeds organismal capacity to maintain homeostasis, organism survival becomes time-limited and can result in mass mortality events. 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 reemergence of 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. Here, we used a simulation approach to understand the effects of a suite of MHW profiles on organism survival probability across 1) thermal tolerance adaptation strategies, 2) interannual temperature variation, and 3) seasonal timing of MHWs. We identified survival isoclines across MHW magnitude and duration broadly connecting acute (low duration-high magnitude) and chronic (long duration-low magnitude) events with equivalent lethal effects on marine organisms. While most attention has been given to chronic MHW events, we show similar lethal effects can be experienced by more common but neglected acute marine heat spikes. Critically, a fixed-baseline definition of MHWs does not accurately categorize biological mortality. By letting organism responses define the extremeness of a MHW event, we can build a mechanistic understanding of MHW effects from a physiological basis. MHW responses can then be transferred across scales of ecological organization and better predict marine ecosystem shifts to MHWs.

Keywords: Ecological forecasting, extreme events, heat stress, mass mortality events, mechanistic ecological models, thermal tolerance, time dependent effects, climate change.

40

Introduction

41

42   With the acceleration of climate change has come an urgent need to understand impact

43 pathways on marine ecosystems. Extreme climate events are hypothesized to have stronger impacts on

44 organisms rather than a shift in mean conditions (Bailey & van de Pol, 2016; Harris et al., 2018). Recently,

45 the increased frequency, intensity, and duration of marine heatwaves (MHWs) have garnered attention

46 as a symptom of climatic warming, with a discrete pulse behavior against the background of chronic

47 warming (Frölicher et al., 2018; Harris et al., 2018; Oliver et al., 2021). Extreme events due to weather

48 stochasticity are naturally occurring events, but as climate change presses temperature distributions

49 upwards these events become more prevalent and increase the probability of lethal effects on organisms

50 (Frölicher et al., 2018; Harvey et al., 2022; Scheffer et al., 2001; Smale et al., 2019). Mass Mortality

51 Events (MMEs) occur when a population of organisms can no longer maintain physiological homeostasis

52 or function (Ern et al., 2023; Ørsted et al., 2022) and are potential sources of population dynamic

53 inflection. Most studies investigating MHW-linked MMEs are descriptive field studies (Fey et al., 2015;

54 Garrabou et al., 2022; Glynn, 1968; Jurgens et al., 2015; Raymond et al., 2022; Tricklebank et al., 2021)

55 that do not investigate how different MHW profiles contribute to MME extent, although newer

56 experimental methods are trying to accommodate realistic MHW profiles (Bernal-Ibáñez et al., 2022;

57 Domínguez et al., 2021; Gerhard et al., 2023; Jentsch et al., 2007; Moyen et al., 2022; Pansch et al.,

58 2018; Seuront et al., 2019).

59   MHW extremeness can be defined using the climatological context in which they occur (Bailey &

60 van de Pol, 2016; Hobday et al., 2016). Recent consensus has defined MHWs as discrete periods when

61 temperatures exceed a seasonally varying threshold, which usually is represented by the 90th percentile

62 of historical climatology for five or more consecutive days (Hobday et al., 2016, 2018; Oliver et al., 2021).

63 This 90th percentile is calculated daily and thus varies seasonally, which is relevant in the context of

64 many organisms' phenology and performance throughout a seasonally variable environment (Hobday et

65   al., 2016). Additionally, MHW severity can be categorized and allow for comparison between events of

66   varying intensity, duration, and rate of onset (Hobday et al., 2018), although categorization is

67   determined by intensity only. This approach quantifies extreme conditions within a local spatiotemporal

68   context and approximates what is likely considered extreme by organisms (Oliver et al., 2021).

69   While such a fixed-baseline oceanographic metric is a good tool for understanding broad

70   patterns, it does not provide a clear picture of how extreme heat affects organisms and ecosystems

71   across scales. For example, organismal abilities to withstand MHWs vary greatly depending on

72   physiology, behavior, function, and thermal niche within an environment (Harris et al., 2018; Smith et

73   al., 2023). Further, a climatological definition of MHWs is only relevant when long-term data are

74   available at the scale relevant to an organism, which can vary widely from millimeters to thousands of

75   kilometers (Bates et al., 2018; Helmuth, 2009; Helmuth et al., 2014). Finally, a five-day minimum

76   threshold duration for a MHW ignores extreme heat events that do occur on much shorter timescales in

77   marine systems (Bates et al., 2018; White et al., 2023), although these shorter events may arise due to

78   interactions between oceanographic and atmospheric processes (Holbrook et al., 2019, 2020). Adhering

79   exclusively to an oceanographic definition of MHWs fails to consider biological responses to MHWs

80   (Smith et al., 2023) and how organismal responses are shaped by their environment. Conversely,

81   experiments and models that describe physiological responses to temperature rarely capture variability

82   found in MHWs and rely on responses to mean conditions, thereby ignoring non-linear responses and

83   the effects of Jensen's inequality (Buckley & Kingsolver, 2021; Dowd et al., 2015; Gerhard et al., 2023;

84   Harris et al., 2018; Morash et al., 2018). We lack coherent models that mechanistically link MHWs to

85   observed responses in organisms and ecosystems (González-Trujillo et al., 2023; van de Pol et al., 2017).

86   A mechanistic model of organism mortality in response to MHWs needs to accommodate

87   variation in the magnitude (or intensity) and duration of a heat challenge. Existing metrics that account

88   for heat duration include cumulative intensity metrics, such as those used in remote-sensed coral reef

89 bleaching tracking products (e.g. Coral Reef Watch, Heron et al., 2016; McClanahan, 2022; Skirving et al.,

90 2020). However, such approaches still rely on static thresholds over which to calculate stress

91 accumulation. A significant mechanistic development towards predicting the lethal effects of MHWs has

92 been the re-emergence of the thermal death time (TDT) model of ectotherm thermal tolerance – a

93 model that predicts death as a function of thermal exposure magnitude and time (Rezende et al., 2014).

94 This model conceptualizes thermal challenge as a heat-dose, and better unifies the relationship between

95 duration and magnitude of exposure that occur in heatwaves (Neuner & Buchner, 2023). When these

96 TDT curves are combined with survival probability functions, a thermal tolerance landscape is produced

97 which conceptualizes survival probability as a continuous response to temperature and temporal

98 exposure (Rezende et al., 2014). Dynamic tolerance models can be built around thermal tolerance

99 landscapes (Jørgensen et al., 2019, 2021; Rezende et al., 2020) to predict survival probability over

100 varying temperature exposures within an organism's environment. Dynamic tolerance models therefore

101 account for time-dependent effects of heat stress. An important prediction of these models is death at

102 relatively benign temperature magnitudes and extended temporal exposures, which are generally

103 unaccounted for in single measures of thermal tolerance, such as CT_{max} and LT_{50}. Therefore, dynamic

104 tolerance models may identify cryptic mortality events that are not predicted by static thermal tolerance

105 indices.

106   The dynamic tolerance model approach is likely to produce more accurate predictions of

107 organism mortality within an environmental context and has shown promise in scaling the physiological

108 effects of climate change across ecological scales. Dynamic tolerance models predicted mortality events

109 with current and future water temperature scenarios in Venice Lagoon bivalves (Bertolini et al., 2023),

110 Antarctic marine invertebrates (Carter et al., 2023; Molina et al., 2022), and lotic amphipods (Verberk et

111 al., 2023). There has been a single application of dynamic tolerance models to MHWs that explicitly

112 investigated the potential for mismatches between categorization based on the 90th percentile of

113   climatology and modelled mortality (Bertolini & Pastres, 2021). A robust investigation of the interface of

114   both dynamic tolerance models and MHW categorization would further the field's ability to

115   mechanistically quantify MHW strength and better forecast ecological responses.

116   Here, we present a generalized computer MHW simulation that seeks to understand how

117   organism mortality responds to variation in MHW duration and magnitude, and how a dynamic

118   tolerance approach compares to Hobday's fixed-baseline categorization of MHW extremity. We first

119   simulate a suite of simple MHWs that vary in magnitude and duration following the threshold-duration

120   definition of Hobday et al. (2016) to explore all MHW possibilities relative to long-term climatological

121   baseline. We then simulate the exposure of two hypothetical organisms with different thermal strategies

122   to each MHW time series using dynamic tolerance models to extract final probability estimates of

123   organism mortality. We show how categorizing MHWs from the resulting survival landscape results in a

124   biologically-informed assessment of MHW lethal impacts that can better guide *ad hoc* classifications of

125   MHW impacts for species of interest. We hypothesize that similar levels of mortality can occur across

126   MHW climatology categories and levels of interannual variation, which may mean a climatology

127   definition of MHWs can both over- and under-estimate ecosystem impacts. Furthermore, a biological

128   approach will correctly predict low mortality during non-summer MHWs.

Methods

129

Simulation of MHW Profiles

130

131   We first constructed a suite of MHWs with varying magnitude and duration parameters. Hobday et al. (

132   2016) define three main MHW parameters: magnitude (thermal intensity), duration (temporal length of

133   MHW above 90th percentile), and rate of onset/decline (slope value between maximum intensity and

134   beginning/end of climatological heatwave) (Figure 1A). We defined duration as the MHW length as it

135   departs from the climatological curve, not the 90% threshold. We adopted this definition because we

136   simulated our time series as sinusoidal curves with no stochastic function, focusing on the main effect of

137   an idealized MHW on mortality. We did not manipulate rate of onset/decline as an independent

138   parameter of magnitude and duration, as this would require introducing a second MHW geometry

139   (trapezoidal) and is not aligned with our main research questions.

140   We simulated MHWs that ranged in duration from one hour to 30 days, with a discrete timestep

141   of one day. We investigated MHW duration shorter than the Hobday et al. (2016) threshold of five days

142   ('marine heat spikes') because of several case studies of organismal mortality in heatwave conditions

143   that last less than five days (Bates et al., 2018; Glynn, 1968; Raymond et al., 2022), although the

144   attribution of these events solely to marine heatwaves rather than atmospheric heatwaves or their

145   interaction may not be possible (Amaya et al., 2020; Holbrook et al., 2019, 2020). Next, we simulated

146   MHWs ranging in magnitude from 0-8°C with discrete breaks of 0.5°C. We chose 8°C as our maximum

147   magnitude, as this encapsulates the magnitudes of the most intense observed MHWs (Hobday et al.,

148   2018; Holbrook et al., 2019). In total, we simulated 527 distinct MHW profiles across magnitude-duration

149   parameters (Supplementary Figure 1).

150   We added each MHW to 52 days of a simulated temperature time series, composed of a

151   sinusoidal curve with an annual mean of 12°C and an annual variation of 14°C. Annual time series

152   maxima occurred on August 17th, and minima on February 15th. This approximates a temperature profile

153   found in temperate estuarine environments in the northern hemisphere. We next added three different

154   thresholds on top of this curve, representing scenarios where 90% of interannual temperature variation

155   occurred within 0.25°C, 0.75°C, and 1.5°C above annual mean temperature (climatology). Using the

156   MHW categorization developed by Hobday et al. (2018), we assigned three additional thresholds for

157   each variation scenario that were 1x, 2x, 3x, and 4x the difference between climatology and the 90%

158   MHW threshold to give moderate, strong, severe, and extreme categorizations (Figure 1A).

159   To demonstrate seasonal timing effects on survival form MHWs, we simulated MHWs across ten

160   time points 90 days after the annual maximum on August 17th. We allowed MHW magnitude to vary

161   between 0°C and 8°C, but fixed duration at 24 days. The 90% threshold was set at 0.75°C above

162   climatological mean. This totaled 153 simulations for the seasonal occurrence portion of the analysis. In

163   total, we simulated 2,261 unique temperature time series across season magnitude-duration

164   parameters, seasonal variability, and seasonal timing.

165   **Simulation of Thermal Death Time Curves**

166   Thermal Death Time (TDT) curves model the time-dependent effects of temperature exposure on

167   organismal thermal tolerance (Rezende et al., 2014). Time to death at a given temperature is determined

168   by a log linear relationship with time of exposure:

$$T_{ko} = CT_{max} - zlog_{10}t, \qquad\qquad \text{Eqn. 1}$$

169   where T_{ko} is the time to knockout (or death), CT_{max} is the acute thermal tolerance at $zlog_{10}t = 0$,

170   which by definition is the thermal tolerance at 1 minute of exposure, z is a species-specific scaling

171   constant representing the inverse slope of the relationship between temperature and log time, and t is

172   time (eqn. 1, Figure 1B). From a TDT curve and the empirical measures of time to death that it describes,

173   we constructed thermal tolerance landscapes. These landscapes start from the assumption that a TDT

174   curve is simply a 50% survival isocline, and the spread of empirical time to death for a given temperature

175   can be used to construct additional mortality probability isoclines (Rezende et al., 2014). Combining

176   survival isoclines together results in a three-dimensional thermal tolerance landscape that fully describes

177   the continuous interactions of time and temperature exposure on probability of death (Rezende et al.,

178   2014).

179   We simulated two hypothetical species' TDT modes with two different parameter sets that

180   reflect two hypothetical thermal adaptation strategies (Supplementary Figure 2). We simulated a chronic

181   tolerator organism that maximizes extended exposure tolerance ($z = 4.5$) against a tradeoff of low acute

182   tolerance (CT_{max} = 45°C), and an acute tolerator that maximizes acute tolerance (CT_{max} = 46°C) at the

183   expense of rapidly decaying tolerance over time ($z = 5.25$). The temperature at which these two

184   strategies have equal responses occurs at their intersection (Supplementary Figure 2). Using the z and

185   CT_{max} parameters for each hypothetical species, we simulated empirical time to death for each species'

186   log-linear model. We simulated ten individuals per temperature treatment (26-46°C, by 2°C, total of 11

187   temperature treatments) following a normal distribution wherein mean time to death occurred at the

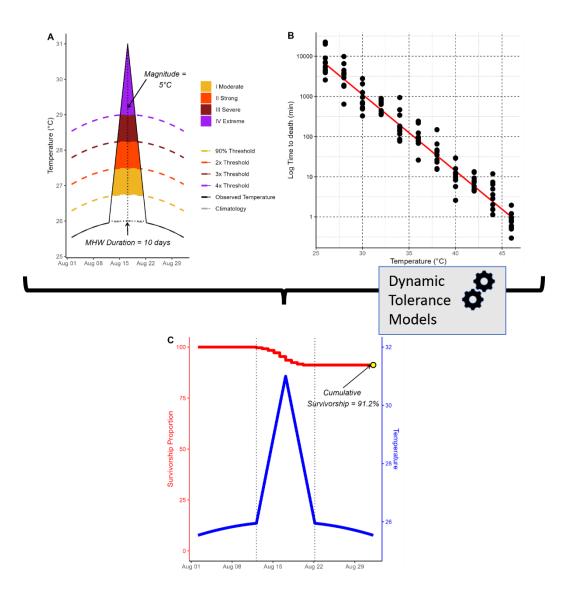188   line of fit and error given as standard error = 0.1°C.

189   **Implementation of Dynamic Tolerance Models**

190   Dynamic tolerance models integrate TDT data and environmental temperature time series to

191   give a cumulative survival estimate at the end of the time series (Figure 1C, Supplementary Text). We

192   added an additional parameter within our *ad hoc* functions adapted from Rezende model (Rezende et

193   al., 2020) to account for the proposed critical temperature (T_c) delineating the limit of organismal

194   maintenance of homeostasis and function (Jørgensen et al., 2021; Ørsted et al., 2022; H.-O. Pörtner,

195   2010). Adding this extra parameter to the Rezende method avoids the accumulation of mortality at

196   theoretically sublethal temperatures, which is not controlled for in this method. In our simulation, we set

197   T_c = 26°C as this is the mean maximum temperature experienced by our hypothetical organisms and

198   within each organism's adaptive capacity. Additionally, we assumed no nightly or tidal immersion stress

199   recovery of organisms during each MHW.

200   **Calculation of MHW Mortality and MHW Mortality Heatmaps**

201   We calculated cumulative mortality for each MHW simulation and extracted the survival at the

202   end of the exposure period (Figure 1C) using the *ad-hoc* Rezende dynamic tolerance model

203   parameterized by one of the two hypothetical species TDT curves (Rezende et al., 2020). In addition, we

204   used adjusted functions to accommodate hourly time series from the heatwaveR package (Schlegel &

205   Smit, 2018) to categorize each simulated MHW according to the statistical oceanographic definition

206   (Hobday et al., 2018). We performed all analyses in R (v. 4.2.2).

207

Figure 1. Conceptual diagram of survival calculation over a MHW simulation using thermal death time (TDT) curves and dynamic tolerance model (Rezende et al., 2020). A) A simulated MHW displaying methods of parametrization using magnitude and duration (black dotted lines). Colored lines indicate MHW severity thresholds, colored areas the portion of the MHW profile within MHW categories. This MHW is considered 'extreme' under the Hobday definition. Climatology line (gray) indicates the historical time series over which thresholds are calculated. B) A TDT curve for a hypothetical species of CT_{max}= 46 °C, z =5.25. The line of fit is determined via linear regression on logarithmically transformed data. Points are simulated data (see Methods) 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 91.2% for that given MHW parametrization of magnitude and duration. Dotted vertical lines indicate the beginning and end of the MHW. This process is repeated for each simulated MHW.

Results

The heatmap of survival between two hypothetical species revealed a substantial impact of different organismal 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 2A). 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 56.3% (Figure 2B, 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 0-18.8%) (Figure 2B, right panel). The acute tolerator experienced up to 10.7% total mortality outside of Hobday categorized MHWs, mostly over MHWs shorter than five days.
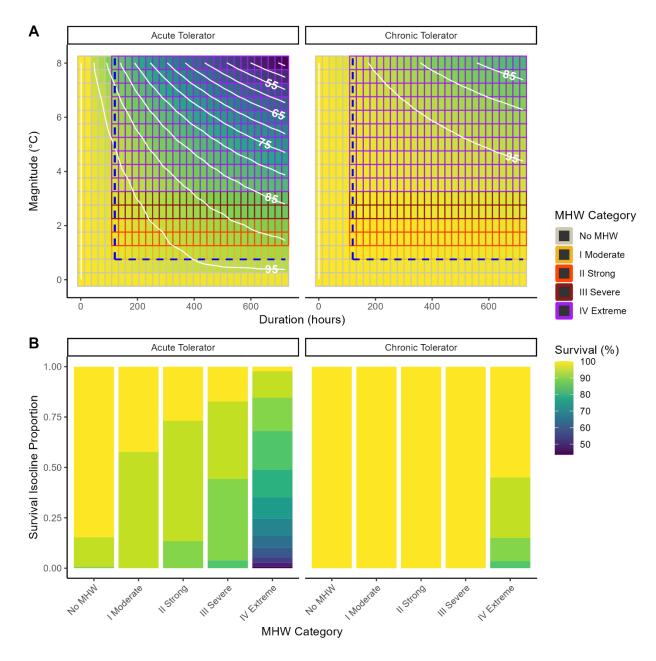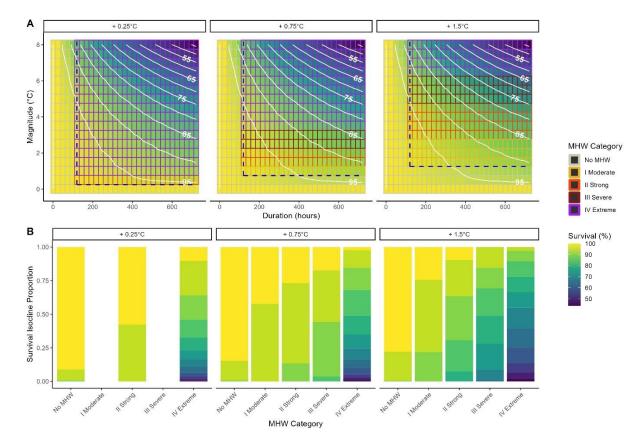
Figure 2A) Survival varies with magnitude and duration between two species and crosses over fixed-baseline MHW categories. Grid color indicates category of MHW, heatmap color the final survival prediction from each MHW. White isoclines connect MHW magnitude-duration combinations that resulted in equal survival. Vertical blue lines indicate the boundary between Hobday-defined MHWs and Marine Heat Spikes (< 5 days). Horizontal blue lines indicate the magnitude at which a temperature event becomes an MHW. B) Proportion of survival predictions, rounded to the nearest 0.05, within each MHW category for two different hypothetical species. Acute tolerator species CT_{max} =46°C , z = 5.25, chronic tolerator CT_{max} =45°C, z = 4.5.
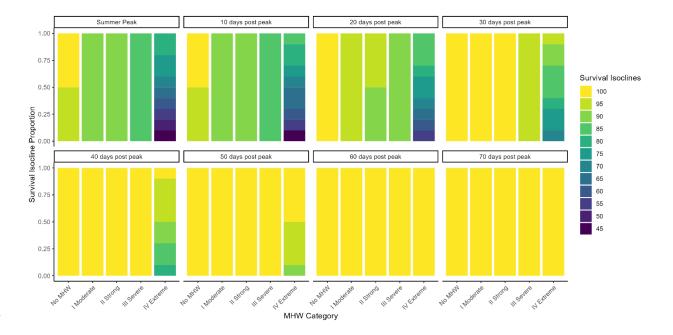
241   Changing interannual variation did not impact the survival heatmap for the acute tolerator

242   species examined, as this altered only the climatological history and thus where Hobday's 90%

243   thresholds were calculated (Figure 3A). The simulated MHW profiles over which dynamic tolerance

244   models predict survival did not change. Decreasing interannual variation increased the number of MHW

245   profiles that were categorized under more extreme categories (Figure 3A , +0.25 °C), while increasing

246   variation decreased the number of MHW scenarios classified as such (Figure 3A, +1.5 °C). In low

247   variation scenarios, the magnitude between MHW category thresholds were smaller than the magnitude

248   steps in our simulations, and so no simulations were categorized as Moderate or Severe (Figure 3B, +0.25

249   °C**Error! Reference source not found.**). With increased annual variation (Figure 3B , +1.5°C), it became

250   less likely that low mortality MHWs would be categorized as extreme for the acute tolerator.

251

Figure 3A) Heatmap of survival predictions for the acute tolerator exposed to simulated MHWs that occur in three distinct varying environments. Labels indicate the degrees above climatology at which the threshold of MHW classification starts. Grid line color indicates category of MHW, heatmap color the final survival prediction from each MHW. White isoclines connect MHW magnitude-duration combinations with equal survival. Vertical blue lines indicate the boundary between Hobday-defined MHWs and Marine Heat Spikes (< 5 days). Horizontal blue lines indicate the magnitude at which a temperature event becomes a Hobday categorized MHW. B) Proportion of survival predictions, rounded to nearest 0.05, within each MHW category for three different variable environments. The middle panels (+0.75°C) are the same as the left-side panels in Figure 2.

Maximum mortality for the acute tolerator across all MHW simulations of magnitude was reached at the seasonal maxima (centered August 17th, Figure 4). Survival increased following the sinusoidal function composing the annual time series for a given magnitude (Supplementary Figure 3), with no mortality occurring after 70 days over even the highest magnitude MHWs.

Figure 4. 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. Not shown are 80- and 90-day plots, which experienced no mortality over all MHW profiles.

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 climatology (Hobday et al., 2016) in tandem 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 five-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 oceanographic definition. We demonstrated that TDT

curve shape and MHW seasonality can yield diverging survival estimates over MHWs within the same

283   Hobday category. Further, a climatological approach is sensitive to historical climatological variability and

284   can over- or under-predict biological impacts.

285   In our MHW simulations, mortality tended to be low in the least severe categories, but the range

286   of survival became broader in more severe categories. In some cases, no mortality was predicted to

287   occur in the most extreme MHWs, reflecting the gap between climatologically anomalous events and

288   events that cause mortality. In other cases, mortality occurred in uncategorized temperature profiles,

289   particularly during events shorter than five days that are otherwise ignored as MHWs. Application of the

290   dynamic tolerance model to bivalves in the Venice Lagoon also found mismatches in the climatological

291   categorization of MHWs and predicted survival. Clams experienced mortality during conditions that did

292   not exceed the 90th percentile climatology threshold, and also a lack of mortality during conditions that

293   did exceed this threshold (Bertolini & Pastres, 2021).

294   A common result across manipulations was the underlying logarithmic shape of survival isoclines

295   over the heatmap (Figures 2A and 3A). This is due to the shape of the TDT response curve reflected

296   through our MHW simulations (Rezende et al., 2014). By connecting MHW scenarios with equal survival,

297   we show that MHWs with different profiles can have similar biological effects. In particular, these

298   isoclines indicate acute events (high magnitude-long duration) to have similar effects as chronic (low

299   magnitude-long duration) events. However, survival over chronic events tends to be proportionally

300   driven by the magnitude of the event, while survival during acute events is more proportionally

301   governed by the duration of the event. While this may seem to support the approach of categorizing

302   MHW impacts based on magnitude in isolation (especially for events longer than five days), short-

303   duration events are common in comparison to long-duration events (Bates et al., 2018; McClanahan et

304   al., 2009; Pietri et al., 2021). The sensitivity of survival to even low durations further indicate the

305   importance of studying acute heating events with parameters such as tidal and daylight cycles, which are

306   neglected using magnitude-only metrics.

307 **TDT curve variation and MHWs**

308 Our analysis simulating the effects of variable MHWs across both species end survival demonstrated that

309 a putatively tolerant species when based on a single-tolerance measure (e.g. CT_{max} in isolation) actually

310 experiences higher mortality across virtually all MHW scenarios tested (Figure 2). The acute tolerator

311 (high CT_{max}, high z) would normally be considered a more tolerant species than the chronic tolerator (low

312 CT_{max}, low z) due to its larger acute thermal limit. However, because the log-linear TDT models intersect

313 and diverge (Supplementary Figure 2), the chronic tolerator is a more tolerant species over lower

314 temperature exposure. Given species with intersecting TDT curves are likely part of the same local

315 species assemblages, such as with marine bivalves and freshwater fish (Bertolini et al., 2023; Troia,

316 2023), the scaling factor z likely plays a more significant role in comparing species and population

317 sensitivities than CT_{max} when considering non-acute MHW events (Rezende et al., 2014). Overall, the role

318 of trade-offs and adaptive strategies of CT_{max}/z is unstudied across taxa and prevents the generalization

319 of organism survival to MHWs. We demonstrated that variation in these parameters has a significant role

320 on organismal tolerance to MHWs, and different adaptive strategies will result in differential organismal

321 outcomes to a shared MHW.

322 **Interannual variation and MHW Categorization**

323 Manipulating interannual seasonal variation did not have a direct impact on organism survival to our

324 simulated MHWs. Instead, increasing climatological variation influences how the 90th percentile of

325 climatology is calculated, and in turn how categories are assigned to MHWs (Hobday et al., 2018). We

326 held the adaptive strategy (i.e. the CT_{max} and z parameters) of our hypothetical organism constant, and as

327 a result the end survival over MHW simulations did not change despite this change in interannual

328 variation. Increasing annual variation tended to mask events with lethal risk by downgrading their

329 categorization. Decreasing variation had the opposite effect of upgrading MHW categorization, lumping

330 MHWs with low and high survival together in extreme categories. These different scenarios should not

331 be interpreted as different potential climate futures; it is expected that variation itself will remain

332 relatively constant with warming (Oliver et al., 2021; Witman et al., 2023). Rather, these different

333 scenarios reflect how temperature variation is itself varied throughout the world's oceans across

334 latitudinal, depth, estuarine, and other gradients (Baumann & Doherty, 2013; Sunday et al., 2011; Thoral

335 et al., 2022; Witman et al., 2023). Organisms in turn can evolve plasticity or adaptive strategies in

336 variable environments or exhibit plasticity and change the shape of their TDT curves (Baumann &

337 Conover, 2011; Somero, 2010; Stillman, 2003; Witman et al., 2023).

338 **Seasonal timing of MHWs**

339 Our analysis found mortality across all MHW simulations decreased with distance from the summer

340 maximum, following the shape of the underlying sine wave describing seasonal temperature variation.

341 Despite mortality essentially approaching zero by mid-October, the severity of MHWs as classified using

342 a climatological approach remained the same. Since the timing of extreme events against the backdrop

343 of the environment is an important modulator of how organisms experience and react to these events,

344 the Hobday MHW framework may fail to approximate biological effects outside of annual extremes

345 (Cinto Mejía & Wetzel, 2023; Ern et al., 2023). MHW timing can influence organism responses by their

346 occurrence against cyclic environmental factors (e.g. seasons, tides) as well as against organism

347 phenology and biological clocks (e.g. spawning, development) (Bernhardt et al., 2020; Giménez, 2023) .

348 Organisms are more likely to experience sublethal effects from MHWs that do not occur over seasonal

349 maxima, and which should be tolerable over moderate magnitudes and durations (Jentsch et al., 2007).

350 Flattening of annual temperature cycles and the elongation of summers may reduce the importance of

351 seasonal MHW timing and enlarge risky periods of stress for organisms (G. Wang & Dillon, 2014; J. Wang

352 et al., 2021). Properly selected TDT data should overcome the sources of variation outlined above by

353 accounting for the ways organisms interact with the timing of extreme events like MHWs.

Limitations and future directions

354

355   As with any modelling framework, applying dynamic tolerance models of thermal tolerance to

356   classifying MHWs has limitations. Thermal tolerance can vary across many contexts and organism states,

357   including acclimation (Stillman, 2003; Terblanche et al., 2007), developmental plasticity (Pottier et al.,

358   2022), life stage and size (Cinto Mejía & Wetzel, 2023; Dahlke et al., 2020; Truebano et al., 2018) ,

359   intraspecific variation (Dwane et al., 2021), seasonal timing (Ern et al., 2023), metabolic state (Guppy &

360   Withers, 1999; Semsar-kazerouni et al., 2020; Vajedsamiei et al., 2021), and oxygen availability (H.-O.

361   Pörtner, 2010; Verberk et al., 2016). Further, we assume mortality from a MHW event is directly

362   attributable to temperature stress. Mortality may also occur due to multiple biotic and abiotic stressors

363   co-occurring with temperature (Buckley & Kingsolver, 2021; Dowd et al., 2015; Ern et al., 2023; Litchman

364   & Thomas, 2023). Even with perfectly chosen TDT curves, behavioral thermoregulation is likely to play a

365   significant role in mediating organism mortality to MHWs (Chapperon & Seuront, 2011; Kearney et al.,

366   2009). Even relatively nonmobile organisms like clams can change their thermal exposure by burrowing

367   deeper into cooler sediment (Domínguez et al., 2021; Macho et al., 2016). Mismatches between

368   predictions and observations and mortality are therefore likely, but predictions of mortality from a single

369   driver can serve as a null model over which stress synergies and covariance effects can be observed

370   (Gerhard et al., 2023; Litchman & Thomas, 2023).

371   In our MHW simulations, we did not include two additional parameters that are likely to mediate

372   organism responses: rate of onset and frequency/return time (Hobday et al., 2016). MHW rate of onset,

373   or ramping rate, is itself a function of magnitude-duration of temperature, and thus has an impact on

374   stress accumulation within an organism (Kingsolver & Umbanhowar, 2018; Rezende et al., 2011, 2020).

375   Further, we did not investigate event frequency, or return time, of MHWs, because dynamic tolerance

376   models do not currently allow for hypothesized organism recovery between MHW events (Jørgensen et

377   al., 2021; Ørsted et al., 2022). Future work could examine the theoretical underpinnings of post-event

378   recovery, as this will likely have a non-linear effect on mortality (Seuront et al., 2019).

379   With these limitations in mind, the Hobday approach to categorizing MHWs requires less

380   parameterization, and remains an important tool for rapidly assessing the potential for ecosystem effects

381   of MHWs. Researchers and managers could consider their goal of assessing MHW strength and consider

382   an alternative approach that considers organismal physiology if ecosystem and organism impacts are the

383   main interest. A recent criticism of the fixed-baseline approach argues that with the ongoing press of

384   warming, MHWs may be calculated to occur for much of the year (Amaya et al., 2023). Shifting the

385   baseline to reflect the warming rate would correct the climatological approach to capture only true

386   anomalous events. However, this approach departs from biological assessments of MHWs with ongoing

387   warming and will not accurately predict ecological impacts.

388   Finally, empirical evidence is needed to support the model results in this analysis. Simulating

389   MHW exposure on an organism and comparing measured mortality with modelled mortality will help

390   clarify the applicability of dynamic tolerance models across taxa and MHW profiles. Within our results,

391   we identified survival isoclines that connect MHW profiles with equal survival. Testing these profiles

392   experimentally and observing where divergences from this expectation occur will help identify any

393   departures from the TDT framework, and ultimately its limitations. Continued work integrating dynamic

394   tolerance models into population, species interaction, and ecosystem models will strengthen the

395   mechanistic basis upon which MHW impacts are forecasted.

Conclusions

397   Building a mechanistic understanding of the physiological effects of MHWs can allow for

398   predictions of MHW effects across scales of ecological organization (Twiname et al., 2020). As MHWs

399   become more predictable (Jacox et al., 2022), forecasting of ecological impacts across scale using

400   workflows like the dynamic tolerance models presented here will become more feasible, thereby helping

401   predict MMEs, population collapse, and species extinction events (Cerini et al., 2023; Verberk et al.,

402   2023). Developing predictive warning systems that can predict ecological climate can give individuals,

403   communities, managers, and governments context-specific information and actionable avoidance,

404   mitigation, or adaptation options.

References

405 **References**

406 Amaya, D. J., Jacox, M. G., Fewings, M. R., Saba, V. S., Stuecker, M. F., Rykaczewski, R. R., Ross, A. C.,

407   Stock, C. A., Capotondi, A., Petrik, C. M., Bograd, S. J., Alexander, M. A., Cheng, W., Hermann, A.

408   J., Kearney, K. A., & Powell, B. S. (2023). Marine heatwaves need clear definitions so coastal

409   communities can adapt. *Nature*, *616*(7955), 29–32. https://doi.org/10.1038/d41586-023-00924-

410   2

411 Amaya, D. J., Miller, A. J., Xie, S.-P., & Kosaka, Y. (2020). Physical drivers of the summer 2019 North Pacific

412   marine heatwave. *Nature Communications*, *11*(1), Article 1. https://doi.org/10.1038/s41467-

413   020-15820-w

414 Bailey, L. D., & van de Pol, M. (2016). Tackling extremes: Challenges for ecological and evolutionary

415   research on extreme climatic events. *Journal of Animal Ecology*, *85*(1), 85–96.

416   https://doi.org/10.1111/1365-2656.12451

417 Bates, A. E., Helmuth, B., Burrows, M. T., Duncan, M. I., Garrabou, J., Guy-Haim, T., Lima, F., Queiros, A.

418   M., Seabra, R., Marsh, R., Belmaker, J., Bensoussan, N., Dong, Y., Mazaris, A. D., Smale, D., Wahl,

419   M., & Rilov, G. (2018). Biologists ignore ocean weather at their peril. *Nature*, *560*(7718), 299–

420   301. https://doi.org/10.1038/d41586-018-05869-5

421 Baumann, H., & Conover, D. (2011). Adaptation to climate change: Contrasting patterns of thermal-

422   reaction-norm evolution in Pacific versus Atlantic silversides. *Proceedings of the Royal Society B:*

423   *Biological Sciences*, *278*(1716), 2265–2273. https://doi.org/10.1098/rspb.2010.2479

424 Baumann, H., & Doherty, O. (2013). Decadal Changes in the World's Coastal Latitudinal Temperature

425   Gradients. *PLoS One*, *8*(6), e67596. https://doi.org/10.1371/journal.pone.0067596

426 Bernal-Ibáñez, A., Gestoso, I., Ramalhosa, P., Campanati, C., & Cacabelos, E. (2022). Interaction of marine

427   heatwaves and grazing on two canopy-forming algae. *Journal of Experimental Marine Biology*

428   *and Ecology*, *556*, 151795. https://doi.org/10.1016/j.jembe.2022.151795

429   Bernhardt, J. R., O'Connor, M. I., Sunday, J. M., & Gonzalez, A. (2020). Life in fluctuating environments.

430   *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1814), 20190454.

431   https://doi.org/10.1098/rstb.2019.0454

432   Bertolini, C., Glaser, D., Canu, M., & Pastres, R. (2023). Coupling habitat-specific temperature scenarios

433   with tolerance landscape to predict the impacts of climate change on farmed bivalves. *Marine*

434   *Environmental Research*, *188*, 106038. https://doi.org/10.1016/j.marenvres.2023.106038

435   Bertolini, C., & Pastres, R. (2021). Tolerance landscapes can be used to predict species-specific responses

436   to climate change beyond the marine heatwave concept: Using tolerance landscape models for

437   an ecologically meaningful classification of extreme climate events. *Estuarine, Coastal and Shelf*

438   *Science*, *252*, 107284. https://doi.org/10.1016/j.ecss.2021.107284

439   Buckley, L. B., & Kingsolver, J. G. (2021). Evolution of Thermal Sensitivity in Changing and Variable

440   Climates. *Annual Review of Ecology, Evolution, and Systematics*, *52*(1), 563–586.

441   https://doi.org/10.1146/annurev-ecolsys-011521-102856

442   Carter, M. J., García-Huidobro, M. R., Aldana, M., Rezende, E. L., Bozinovic, F., Galbán-Malagón, C., &

443   Pulgar, J. M. (2023). Upper thermal limits and risk of mortality of coastal Antarctic ectotherms.

444   *Frontiers in Marine Science*, *9*, 1108330. https://doi.org/10.3389/fmars.2022.1108330

445   Cerini, F., Childs, D. Z., & Clements, C. F. (2023). A predictive timeline of wildlife population collapse.

446   *Nature Ecology & Evolution*, *7*(3), Article 3. https://doi.org/10.1038/s41559-023-01985-2

447   Chapperon, C., & Seuront, L. (2011). Behavioral thermoregulation in a tropical gastropod: Links to climate

448   change scenarios. *Global Change Biology*, *17*(4), 1740–1749. https://doi.org/10.1111/j.1365-

449   2486.2010.02356.x

450   Cinto Mejía, E., & Wetzel, W. C. (2023). The ecological consequences of the timing of extreme climate

451   events. *Ecology and Evolution*, *13*(1), e9661. https://doi.org/10.1002/ece3.9661

452   Dahlke, F. T., Wohlrab, S., Butzin, M., & Pörtner, H.-O. (2020). Thermal bottlenecks in the life cycle define

453   climate vulnerability of fish. *Science*, *369*(6499), 65–70. https://doi.org/10.1126/science.aaz3658

454   Domínguez, R., Olabarria, C., Woodin, S. A., Wethey, D. S., Peteiro, L. G., Macho, G., & Vázquez, E. (2021).

455   Contrasting responsiveness of four ecologically and economically important bivalves to

456   simulated heat waves. *Marine Environmental Research*, *164*, 105229.

457   https://doi.org/10.1016/j.marenvres.2020.105229

458   Dowd, W. W., King, F. A., & Denny, M. W. (2015). Thermal variation, thermal extremes and the

459   physiological performance of individuals. *Journal of Experimental Biology*, *218*(12), 1956–1967.

460   https://doi.org/10.1242/jeb.114926

461   Dwane, C., Rundle, S. D., Tills, O., Rezende, E. L., Galindo, J., Rolán-Alvarez, E., & Truebano, M. (2021).

462   Divergence in Thermal Physiology Could Contribute to Vertical Segregation in Intertidal Ecotypes

463   of Littorina saxatilis. *Physiological and Biochemical Zoology: PBZ*, *94*(6), 353–365.

464   https://doi.org/10.1086/716176

465   Ern, R., Andreassen, A. H., & Jutfelt, F. (2023). Physiological mechanisms of acute upper thermal

466   tolerance in fish. *Physiology*, physiol.00027.2022. https://doi.org/10.1152/physiol.00027.2022

467   Fey, S. B., Siepielski, A. M., Nusslé, S., Cervantes-Yoshida, K., Hwan, J. L., Huber, E. R., Fey, M. J., Catenazzi,

468   A., & Carlson, S. M. (2015). Recent shifts in the occurrence, cause, and magnitude of animal

469   mass mortality events. *Proceedings of the National Academy of Sciences*, *112*(4), 1083–1088.

470   https://doi.org/10.1073/pnas.1414894112

471   Frölicher, T. L., Fischer, E. M., & Gruber, N. (2018). Marine heatwaves under global warming. *Nature*,

472   *560*(7718), 360–364. https://doi.org/10.1038/s41586-018-0383-9

473   Garrabou, J., Gómez-Gras, D., Medrano, A., Cerrano, C., Ponti, M., Schlegel, R., Bensoussan, N., Turicchia,

474   E., Sini, M., Gerovasileiou, V., Teixido, N., Mirasole, A., Tamburello, L., Cebrian, E., Rilov, G.,

475   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*, gcb.16301.

https://doi.org/10.1111/gcb.16301

Gerhard, M., Koussoroplis, A.-M., Raatz, M., Pansch, C., Fey, S. B., Vajedsamiei, 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., Ptacnik,

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., Russell, B. D., Connell, S. D., Dong, Y., Harley, C. D., Lima, F. P., Sará, G., Williams, G. A., &
Mieszkowska, N. (2014). Beyond long-term averages: Making biological sense of a rapidly
changing world. *Climate Change Responses*, *1*(1), 6. https://doi.org/10.1186/s40665-014-0006-0

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). 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.,

524   Straub, S. C., & Wernberg, T. (2019). A global assessment of marine heatwaves and their drivers.

525   *Nature Communications*, *10*(1), Article 1. https://doi.org/10.1038/s41467-019-10206-z

526   Holbrook, N. J., Sen Gupta, A., Oliver, E. C. J., Hobday, A. J., Benthuysen, J. A., Scannell, H. A., Smale, D. A.,

527   & Wernberg, T. (2020). Keeping pace with marine heatwaves. *Nature Reviews Earth &*

528   *Environment*, *1*(9), Article 9. https://doi.org/10.1038/s43017-020-0068-4

529   Jacox, M. G., Alexander, M. A., Amaya, D., Becker, E., Bograd, S. J., Brodie, S., Hazen, E. L., Pozo Buil, M., &

530   Tommasi, D. (2022). Global seasonal forecasts of marine heatwaves. *Nature*, *604*(7906), Article

531   7906. https://doi.org/10.1038/s41586-022-04573-9

532   Jentsch, A., Kreyling, J., & Beierkuhnlein, C. (2007). A new generation of climate-change experiments:

533   Events, not trends. *Frontiers in Ecology and the Environment*, *5*(7), 365–374.

534   https://doi.org/10.1890/1540-9295(2007)5[365:ANGOCE]2.0.CO;2

535   Jørgensen, L. B., Malte, H., Ørsted, M., Klahn, N. A., & Overgaard, J. (2021). A unifying model to estimate

536   thermal tolerance limits in ectotherms across static, dynamic and fluctuating exposures to

537   thermal stress. *Scientific Reports*, *11*, 12840. https://doi.org/10.1038/s41598-021-92004-6

538   Jørgensen, L. B., Malte, H., & Overgaard, J. (2019). How to assess Drosophila heat tolerance: Unifying

539   static and dynamic tolerance assays to predict heat distribution limits. *Functional Ecology*, *33*(4),

540   629–642. https://doi.org/10.1111/1365-2435.13279

541   Jurgens, L. J., Rogers-Bennett, L., Raimondi, P. T., Schiebelhut, L. M., Dawson, M. N., Grosberg, R. K., &

542   Gaylord, B. (2015). Patterns of Mass Mortality among Rocky Shore Invertebrates across 100 km

543   of Northeastern Pacific Coastline. *PLOS ONE*, *10*(6), e0126280.

544   https://doi.org/10.1371/journal.pone.0126280

545   Kearney, M., Shine, R., & Porter, W. P. (2009). The potential for behavioral thermoregulation to buffer

546   "cold-blooded" animals against climate warming. *Proceedings of the National Academy of*

547   *Sciences*, *106*(10), 3835–3840. https://doi.org/10.1073/pnas.0808913106

548 Kingsolver, J. G., & Umbanhowar, J. (2018). The analysis and interpretation of critical temperatures.

549   *Journal of Experimental Biology*, *221*(12), jeb167858. https://doi.org/10.1242/jeb.167858

550 Litchman, E., & Thomas, M. K. (2023). Are we underestimating the ecological and evolutionary effects of

551   warming? Interactions with other environmental drivers may increase species vulnerability to

552   high temperatures. *Oikos*, *2023*(2), e09155. https://doi.org/10.1111/oik.09155

553 Macho, G., Woodin, S. A., Wethey, D. S., & Vázquez, E. (2016). Impacts of Sublethal and Lethal High

554   Temperatures on Clams Exploited in European Fisheries. *Journal of Shellfish Research*, *35*(2),

555   405–419. https://doi.org/10.2983/035.035.0215

556 McClanahan, T. R. (2022). Coral responses to climate change exposure. *Environmental Research Letters*,

557   *17*(7), 073001. https://doi.org/10.1088/1748-9326/ac7478

558 McClanahan, T. R., Ateweberhan, M., Omukoto, J., & Pearson, L. (2009). Recent seawater temperature

559   histories, status, and predictions for Madagascar's coral reefs. *Marine Ecology Progress Series*,

560   *380*, 117–128. https://doi.org/10.3354/meps07879

561 Molina, A. N., Pulgar, J. M., Rezende, E. L., & Carter, M. J. (2022). Heat tolerance of marine ectotherms in

562   a warming Antarctica. *Global Change Biology*, *n/a*(n/a). https://doi.org/10.1111/gcb.16402

563 Morash, A. J., Neufeld, C., MacCormack, T. J., & Currie, S. (2018). The importance of incorporating natural

564   thermal variation when evaluating physiological performance in wild species. *Journal of*

565   *Experimental Biology*, *221*(14), jeb164673. https://doi.org/10.1242/jeb.164673

566 Moyen, N. E., Somero, G. N., & Denny, M. W. (2022). Effects of heat acclimation on cardiac function in

567   the intertidal mussel Mytilus californianus: Can laboratory-based indices predict survival in the

568   field? *The Journal of Experimental Biology*, *225*(9), jeb243050.

569   https://doi.org/10.1242/jeb.243050

570   Neuner, G., & Buchner, O. (2023). The dose makes the poison: The longer the heat lasts, the lower the

571   temperature for functional impairment and damage. *Environmental and Experimental Botany*,

572   *212*, 105395. https://doi.org/10.1016/j.envexpbot.2023.105395

573   Oliver, E. C. J., Benthuysen, J. A., Darmaraki, S., Donat, M. G., Hobday, A. J., Holbrook, N. J., Schlegel, R.

574   W., & Sen Gupta, A. (2021). Marine Heatwaves. *Annual Review of Marine Science*, *13*(1), 313–

575   342. https://doi.org/10.1146/annurev-marine-032720-095144

576   Ørsted, M., Jørgensen, L. B., & Overgaard, J. (2022). Finding the right thermal limit: A framework to

577   reconcile ecological, physiological and methodological aspects of CTmax in ectotherms. *Journal*

578   *of Experimental Biology*, *225*(19), jeb244514. https://doi.org/10.1242/jeb.244514

579   Pansch, C., Scotti, M., Barboza, F. R., Al-Janabi, B., Brakel, J., Briski, E., Bucholz, B., Franz, M., Ito, M.,

580   Paiva, F., Saha, M., Sawall, Y., Weinberger, F., & Wahl, M. (2018). Heat waves and their

581   significance for a temperate benthic community: A near-natural experimental approach. *Global*

582   *Change Biology*, *24*(9), 4357–4367. https://doi.org/10.1111/gcb.14282

583   Pietri, A., Colas, F., Mogollon, R., Tam, J., & Gutierrez, D. (2021). Marine heatwaves in the Humboldt

584   current system: From 5-day localized warming to year-long El Niños. *Scientific Reports*, *11*,

585   21172. https://doi.org/10.1038/s41598-021-00340-4

586   Pörtner, H. O., & Knust, R. (2007). Climate Change Affects Marine Fishes Through the Oxygen Limitation

587   of Thermal Tolerance. *Science*, *315*(5808), 95–97. https://doi.org/10.1126/science.1135471

588   Pörtner, H.-O. (2010). Oxygen- and capacity-limitation of thermal tolerance: A matrix for integrating

589   climate-related stressor effects in marine ecosystems. *Journal of Experimental Biology*, *213*(6),

590   881–893. https://doi.org/10.1242/jeb.037523

591   Pottier, P., Burke, S., Zhang, R. Y., Noble, D. W. A., Schwanz, L. E., Drobniak, S. M., & Nakagawa, S. (2022).

592   Developmental plasticity in thermal tolerance: Ontogenetic variation, persistence, and future

593   directions. *Ecology Letters*, *25*(10), 2245–2268. https://doi.org/10.1111/ele.14083

594   Raymond, W. W., Barber, J. S., Dethier, M. N., Hayford, H. A., Harley, C. D. G., King, T. L., Paul, B., Speck, C.

595   A., Tobin, E. D., Raymond, A. E. T., & McDonald, P. S. (2022). Assessment of the impacts of an

596   unprecedented heatwave on intertidal shellfish of the Salish Sea. *Ecology*, *n/a*(n/a), e3798.

597   https://doi.org/10.1002/ecy.3798

598   Rezende, E. L., Bozinovic, F., Szilágyi, A., & Santos, M. (2020). Predicting temperature mortality and

599   selection in natural Drosophila populations. *Science*, *369*(6508), 1242–1245.

600   https://doi.org/10.1126/science.aba9287

601   Rezende, E. L., Castañeda, L. E., & Santos, M. (2014). Tolerance landscapes in thermal ecology. *Functional*

602   *Ecology*, *28*(4), 799–809. https://doi.org/10.1111/1365-2435.12268

603   Rezende, E. L., Tejedo, M., & Santos, M. (2011). Estimating the adaptive potential of critical thermal

604   limits: Methodological problems and evolutionary implications. *Functional Ecology*, *25*(1), 111–

605   121. https://doi.org/10.1111/j.1365-2435.2010.01778.x

606   Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., & Walker, B. (2001). Catastrophic shifts in ecosystems.

607   *Nature*, *413*(6856), 591–596. https://doi.org/10.1038/35098000

608   Schlegel, R. W., & Smit, A. J. (2018). heatwaveR: A central algorithm for the detection of heatwaves and

609   cold-spells. *Journal of Open Source Software*, *3*(27), 821. https://doi.org/10.21105/joss.00821

610   Semsar-kazerouni, M., Boerrigter, J. G. J., & Verberk, W. C. E. P. (2020). Changes in heat stress tolerance in

611   a freshwater amphipod following starvation: The role of oxygen availability, metabolic rate, heat

612   shock proteins and energy reserves. *Comparative Biochemistry and Physiology Part A: Molecular*

613   *& Integrative Physiology*, *245*, 110697. https://doi.org/10.1016/j.cbpa.2020.110697

614   Seuront, L., Nicastro, K. R., Zardi, G. I., & Goberville, E. (2019). Decreased thermal tolerance under

615   recurrent heat stress conditions explains summer mass mortality of the blue mussel Mytilus

616   edulis. *Scientific Reports*, *9*(1), Article 1. https://doi.org/10.1038/s41598-019-53580-w

617 Skirving, W., Marsh, B., De La Cour, J., Liu, G., Harris, A., Maturi, E., Geiger, E., & Eakin, C. M. (2020).

618 CoralTemp and the Coral Reef Watch Coral Bleaching Heat Stress Product Suite Version 3.1.

619 *Remote Sensing*, *12*(23), 3856. https://doi.org/10.3390/rs12233856

620 Smale, D. A., Wernberg, T., Oliver, E. C. J., Thomsen, M., Harvey, B. P., Straub, S. C., Burrows, M. T.,

621 Alexander, L. V., Benthuysen, J. A., Donat, M. G., Feng, M., Hobday, A. J., Holbrook, N. J., Perkins-

622 Kirkpatrick, S. E., Scannell, H. A., Sen Gupta, A., Payne, B. L., & Moore, P. J. (2019). Marine

623 heatwaves threaten global biodiversity and the provision of ecosystem services. *Nature Climate*

624 *Change*, *9*(4), 306–312. https://doi.org/10.1038/s41558-019-0412-1

625 Smith, K. E., Burrows, M. T., Hobday, A. J., King, N. G., Moore, P. J., Sen Gupta, A., Thomsen, M. S.,

626 Wernberg, T., & Smale, D. A. (2023). Biological Impacts of Marine Heatwaves. *Annual Review of*

627 *Marine Science*, *15*(1), annurev-marine-032122-121437. https://doi.org/10.1146/annurev-

628 marine-032122-121437

629 Somero, G. N. (2010). The physiology of climate change: How potentials for acclimatization and genetic

630 adaptation will determine "winners" and "losers." *Journal of Experimental Biology*, *213*(6), 912–

631 920. https://doi.org/10.1242/jeb.037473

632 Stillman, J. H. (2003). Acclimation Capacity Underlies Susceptibility to Climate Change. *Science*,

633 *301*(5629), 65. https://doi.org/10.1126/science.1083073

634 Sunday, J. M., Bates, A. E., & Dulvy, N. K. (2011). Global analysis of thermal tolerance and latitude in

635 ectotherms. *Proceedings: Biological Sciences*, *278*(1713), 1823–1830.

636 https://doi.org/10.1098/rspb.2010.1295

637 Tang, J., & Mitcham, E. (Eds.). (2007). *Heat treatments for postharvest pest control: Theory and practice*.

638 CABI.

639   Terblanche, J. S., Deere, J. A., Clusella-Trullas, S., Janion, C., & Chown, S. L. (2007). Critical thermal limits

640   depend on methodological context. *Proceedings of the Royal Society B: Biological Sciences*,

641   *274*(1628), 2935–2943. https://doi.org/10.1098/rspb.2007.0985

642   Thoral, F., Montie, S., Thomsen, M. S., Tait, L. W., Pinkerton, M. H., & Schiel, D. R. (2022). Unravelling

643   seasonal trends in coastal marine heatwave metrics across global biogeographical realms.

644   *Scientific Reports*, *12*(1), Article 1. https://doi.org/10.1038/s41598-022-11908-z

645   Tricklebank, K. A., Grace, R. V., & Pilditch, C. A. (2021). Decadal population dynamics of an intertidal

646   bivalve (*Austrovenus stutchburyi*) bed: Pre- and post- a mass mortality event. *New Zealand*

647   *Journal of Marine and Freshwater Research*, *55*(2), 352–374.

648   https://doi.org/10.1080/00288330.2020.1772323

649   Troia, M. J. (2023). Magnitude–duration relationships of physiological sensitivity and environmental

650   exposure improve climate change vulnerability assessments. *Ecography*, *2023*(1), e06217.

651   https://doi.org/10.1111/ecog.06217

652   Truebano, M., Fenner, P., Tills, O., Rundle, S. D., & Rezende, E. L. (2018). Thermal strategies vary with life

653   history stage. *The Journal of Experimental Biology*, *221*(8), jeb171629.

654   https://doi.org/10.1242/jeb.171629

655   Twiname, S., Audzijonyte, A., Blanchard, J. L., Champion, C., de la Chesnais, T., Fitzgibbon, Q. P., Fogarty,

656   H. E., Hobday, A. J., Kelly, R., Murphy, K. J., Oellermann, M., Peinado, P., Tracey, S., Villanueva, C.,

657   Wolfe, B., & Pecl, G. T. (2020). A cross-scale framework to support a mechanistic understanding

658   and modelling of marine climate-driven species redistribution, from individuals to communities.

659   *Ecography*, *43*(12), 1764–1778. https://doi.org/10.1111/ecog.04996

660   Vajedsamiei, J., Wahl, M., Schmidt, A. L., Yazdanpanahan, M., & Pansch, C. (2021). The Higher the Needs,

661   the Lower the Tolerance: Extreme Events May Select Ectotherm Recruits With Lower Metabolic

662   Demand and Heat Sensitivity. *Frontiers in Marine Science*, *8*.

663   https://www.frontiersin.org/articles/10.3389/fmars.2021.660427

664 van de Pol, M., Jenouvrier, S., Cornelissen, J. H. C., & Visser, M. E. (2017). Behavioural, ecological and

665   evolutionary responses to extreme climatic events: Challenges and directions. *Philosophical*

666   *Transactions of the Royal Society B: Biological Sciences*, *372*(1723), 20160134.

667   https://doi.org/10.1098/rstb.2016.0134

668 Verberk, W. C. E. P., Hoefnagel, K. N., Peralta-Maraver, I., Floury, M., & Rezende, E. L. (2023). Long-term

669   forecast of thermal mortality with climate warming in riverine amphipods. *Global Change*

670   *Biology*, *n/a*(n/a). https://doi.org/10.1111/gcb.16834

671 Verberk, W. C. E. P., Overgaard, J., Ern, R., Bayley, M., Wang, T., Boardman, L., & Terblanche, J. S. (2016).

672   Does oxygen limit thermal tolerance in arthropods? A critical review of current evidence.

673   *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *192*, 64–

674   78. https://doi.org/10.1016/j.cbpa.2015.10.020

675 Wang, G., & Dillon, M. E. (2014). Recent geographic convergence in diurnal and annual temperature

676   cycling flattens global thermal profiles. *Nature Climate Change*, *4*(11), Article 11.

677   https://doi.org/10.1038/nclimate2378

678 Wang, J., Guan, Y., Wu, L., Guan, X., Cai, W., Huang, J., Dong, W., & Zhang, B. (2021). Changing Lengths of

679   the Four Seasons by Global Warming. *Geophysical Research Letters*, *48*(6), e2020GL091753.

680   https://doi.org/10.1029/2020GL091753

681 White, R. H., Anderson, S., Booth, J. F., Braich, G., Draeger, C., Fei, C., Harley, C. D. G., Henderson, S. B.,

682   Jakob, M., Lau, C.-A., Mareshet Admasu, L., Narinesingh, V., Rodell, C., Roocroft, E., Weinberger,

683   K. R., & West, G. (2023). The unprecedented Pacific Northwest heatwave of June 2021. *Nature*

684   *Communications*, *14*(1), Article 1. https://doi.org/10.1038/s41467-023-36289-3
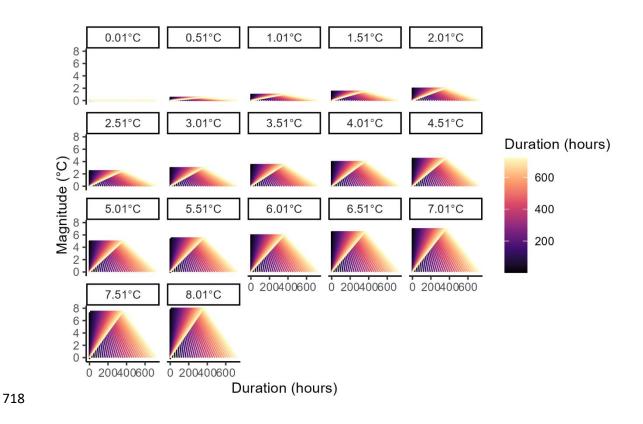
685   Witman, J. D., Pershing, A. J., & Bruno, J. F. (2023). Smooth and Spiky: The Importance of Variability in

686   Marine Climate Change Ecology. *Annual Review of Ecology, Evolution, and Systematics*, *54*(1),

687   129–149. https://doi.org/10.1146/annurev-ecolsys-022323-082123
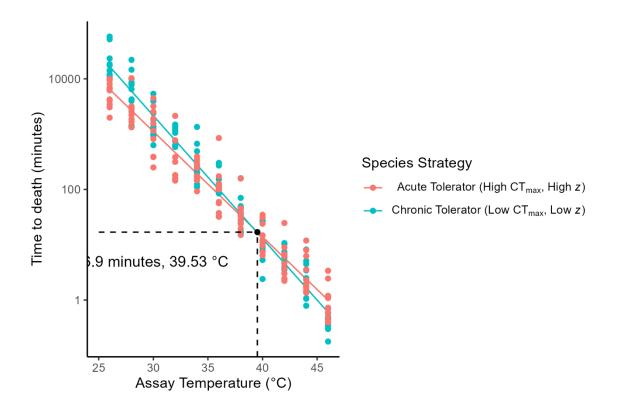
688

689

Supplementary Information

Dynamic Survival Models

Two major dynamic survival models have been recently described that rely on two different methods of calculating the instantaneous rate of mortality for a timestep within the temperature time series. The Rezende method (also called Fundamental Kinetic Model, Rezende et al., 2020; Tang & Mitcham, 2007) iteratively calculates mortality from a series of cumulative survival curves parameterized from the spread of empirical time to death data. The Jørgensen method (also called Degree Minute Models; Jørgensen et al., 2021; Tang & Mitcham, 2007) treats temperatures above a critical temperature (Tc; loss of homeostasis) as a thermal dose correlating with injury accumulation. This method integrates beneath the exposure time series to arrive at a measure of area between the time series and Tc that corresponds to a level of injury accumulation for an organism. An important distinction between the two methods is that the Rezende method does not directly use the fitted log-linear model typically used to describe Thermal Death Time (TDT) curves while the Jørgensen method uses the fitted model directly. The Rezende method may more accurately predict death if different mechanisms are responsible for death at different time-temperature exposures (Ern et al., 2023; Rezende et al., 2014; Tang & Mitcham, 2007). However, since death is calculated from the spread of individual data points of time to death, this method is likely sensitive to precision error arising from methodology. Additionally, the Rezende method does not include the concept of critical temperature (Tc or Tcrit) that delineates organism lifespan and time-limited survival (mortality from heat stress) (Ern et al., 2023; Ørsted et al., 2022; Pörtner & Knust, 2007). While the general mechanisms behind Tc remain unclear (Ørsted et al., 2022), omitting Tc likely results in overestimations of mortality at ecologically realistic temperatures for organism persistence when summed over long time spans. The Jørgensen method is not probability based, includes Tc, and assumes lethal stress is equally accumulated across temperature and time exposures. Therefore, while

713   the Rezende method requires higher sample sizes of empirical data at each temperature point, the

714   Jørgensen method can be used with only the TDT curve, parameterized with a minimum of three data

715   points. Both methods are supported by empirical data, although mostly through the experimental use of

716   Drosophila. Future work should investigate the validity and limitations of both methods in tandem across

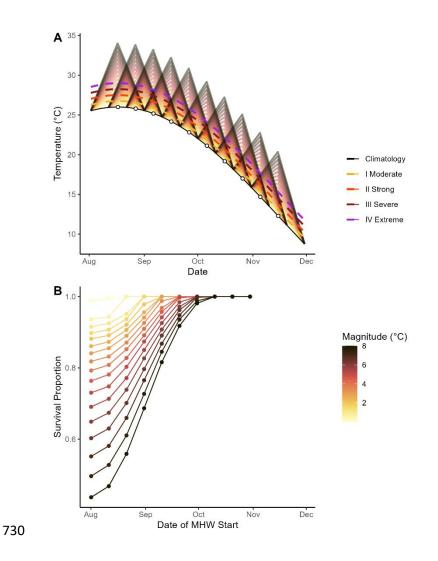717   non-model species.

718

719   Supplementary Figure 1. Array of 527 MHW simulations across 17 durations and 31 durations. Each

720   individual triangle (represented by a single color in each subplot) represents one MHW simulation.

721

722

Supplementary Figure 2. Thermal death time curves for two hypothetical species that follow two

divergent adaptation strategies. One species exhibits an acute tolerator strategy (higher CTmax = 46 °C,

high z value 5.25) than the chronic tolerator (45 °C, 4.5). Because z is the negative inverse of slope, this

translates to a high acute tolerance trading off with a slower rate of time to death increase with lower

exposure temperatures. The intercept of these two points occurs at 16.9 min, 39.5 °C. The chronic

tolerator would exhibit slower time to death than the acute tolerator at temperatures above 39.53°C.

729

730

Supplementary Figure 3A. MHWs of fixed duration (24 days) but variable magnitude (0-8°C) were

simulated across ten time points post annual maximum (white points). Each MHW was simulated onto

the climatological curve 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.

736

Citations form Supplement

737   Ern, R., Andreassen, A. H., & Jutfelt, F. (2023). Physiological mechanisms of acute upper thermal

739   tolerance in fish. *Physiology*, physiol.00027.2022. https://doi.org/10.1152/physiol.00027.2022

740   Jørgensen, L. B., Malte, H., Ørsted, M., Klahn, N. A., & Overgaard, J. (2021). A unifying model to estimate

741   thermal tolerance limits in ectotherms across static, dynamic and fluctuating exposures to

742   thermal stress. *Scientific Reports*, *11*, 12840. https://doi.org/10.1038/s41598-021-92004-6

743   Ørsted, M., Jørgensen, L. B., & Overgaard, J. (2022). Finding the right thermal limit: A framework to

744   reconcile ecological, physiological and methodological aspects of CTmax in ectotherms. *Journal*

745   *of Experimental Biology*, *225*(19), jeb244514. https://doi.org/10.1242/jeb.244514

746   Pörtner, H. O., & Knust, R. (2007). Climate Change Affects Marine Fishes Through the Oxygen Limitation

747   of Thermal Tolerance. *Science*, *315*(5808), 95–97. https://doi.org/10.1126/science.1135471

748   Rezende, E. L., Bozinovic, F., Szilágyi, A., & Santos, M. (2020). Predicting temperature mortality and

749   selection in natural Drosophila populations. *Science*, *369*(6508), 1242–1245.

750   https://doi.org/10.1126/science.aba9287

751   Rezende, E. L., Castañeda, L. E., & Santos, M. (2014). Tolerance landscapes in thermal ecology. *Functional*

752   *Ecology*, *28*(4), 799–809. https://doi.org/10.1111/1365-2435.12268

753   Tang, J., & Mitcham, E. (Eds.). (2007). *Heat treatments for postharvest pest control: Theory and practice*.

754   CABI.

755