

Title:

Heat tolerance and its plasticity in freshwater and marine fishes are linked to their thermal regimes.

Authors:

Wilco C.E.P. Verberk¹, Erin Henry², Félix P. Leiva^{1,3}, Valerio Barbarossa^{4,5}, Aafke M. Schipper^{1,5}

Author's ORCID iDs:

Wilco C. E. P. Verberk: 0000-0002-0691-583X

Erin Henry: 0000-0002-4461-6697

Felix P. Leiva: 0000-0003-0249-9274

Valerio Barbarossa: 0000-0002-0519-6968

Aafke M. Schipper: 0000-0002-5667-0893

Institutional affiliations:

1 RIBES, Radboud University, Nijmegen, The Netherlands

2 WUR, Wageningen University and Research, Wageningen, the Netherlands

3 Department of Integrative Ecophysiology, Alfred Wegener Institute Helmholtz Centre Polar and Marine Research (AWI), 27570, Bremerhaven, Germany

4 Institute of Environmental Sciences, Leiden University, Leiden, The Netherlands

5 PBL Netherlands Environmental Assessment Agency, The Hague, The Netherlands

Abstract

Responses to climate change are rooted in thermal physiology, and many studies have focussed on heat tolerance and plasticity of heat tolerance. Latitudinal patterns in heat tolerance are commonly considered to reflect latitudinal differences in thermal regimes, but direct tests are few. Here we show that the extremes and fluctuations in habitat temperature explain variation in heat tolerance of freshwater and marine fishes. Furthermore, we found that freshwater fish exhibit greater plasticity in heat tolerance than their marine counterparts. This reflects that, compared to marine fishes, freshwater fishes are exposed to greater thermal fluctuations. Our findings underscore the importance of thermal physiology for predicting responses to climate change and highlight that plasticity in heat tolerance is an important mechanism to cope with thermal extremes, especially for organisms living in thermally variable habitats such as freshwater fish.

Introduction

Earth's climate is warming, exposing its biota to increasingly higher and more variable temperatures (IPCC, 2018). Biological responses to this human-induced warming include range shifts and changes in phenology to track thermal niches (Lenoir et al., 2020; Sunday et al., 2012). Large-scale syntheses of how well organisms can tolerate thermal extremes typically yield strong latitudinal clines and patterns that are different for organisms from aquatic and terrestrial realms (Pinsky et al., 2019). Contrasts in maximum habitat temperatures and thermal variability between realms and across latitudes are used to explain such patterns in heat tolerance (Sunday et al., 2019). However, such comparisons frequently involve aquatic and terrestrial organisms that also differ in other respects, such as mode of breathing and evolutionary history, which are known to affect heat tolerance (Bennett et al., 2021; Leiva et al., 2019; Verberk et al., 2016). Furthermore, plasticity in heat tolerance, i.e. the ability of individuals to modulate their heat tolerance level via acclimation, is also expected to vary with the thermal regime of their habitat (Stillman, 2003; Verberk et al., 2018). Organisms in habitats that are thermally variable are expected to exhibit a higher plasticity of heat tolerance than those from thermally stable habitats (Bozinovic et al., 2011; Gunderson & Stillman, 2015). Latitude is frequently used as a proxy for both heat (highest in tropical regions) and thermal variability (highest in temperate regions) (Chown et al., 2004). However, at a given latitude thermal regime can vary considerably longitudinally and few studies explicitly include habitat thermal maxima let alone thermal variability (Sunday et al., 2019).

The advent of global water temperature models (Barbarossa et al., 2021; Wanders et al., 2019) and datasets (e.g. NOAA Global Surface Temperature Dataset) offers the opportunity to test whether and how large-scale patterns in heat tolerance and plasticity therein are related to the thermal regime that organisms are exposed to. Here we explore relationships between upper thermal limits and thermal regimes for fishes, the most diverse group of vertebrates which occur in both marine and freshwater habitats across the globe. The advantage of using a single taxonomic group with gill breathing as the single most important mode of respiration reduces possible confounding factors that could otherwise drive observed differences in heat tolerance. In addition, including the full range from freshwater habitats to and marine habitats allows us to test the idea that differences in thermal exposure in a species' evolutionary history have acted as a selection pressure for the heat sensitivity they exhibit today. More specifically, owing to their smaller volume, temperatures in freshwater bodies (e.g., ponds, lagoons, lakes) have higher diurnal and seasonal fluctuations, and exhibit more extreme values compared to marine habitats. We test whether (i) thermal regime is a better predictor than latitude for basal heat tolerance and plasticity therein and (ii) how heat tolerance varies between freshwater and marine fishes while accounting for evolutionary history. We hypothesize that the greater variability in habitat temperature would be expected to manifest as a greater plasticity in thermal tolerance for freshwater fish.

Methods

Thermal tolerance data collection

We compiled thermal tolerance data from three existing databases: GlobTherm, a global database of experimentally derived thermal tolerance values across various species groups (Bennett et al. 2018), and the databases from two other thermal tolerance studies (Comte and Olden 2017a; Leiva et al. 2019). From these databases, we selected records concerning fish species, and we supplemented these data through an additional literature search for more recent studies (from 2015 onwards),

using the Web of Science search engine and the following search terms: “fish” and “ctmax”, “critical thermal maximum”, “thermal limit”, or “thermal tolerance”. From the search result, we selected papers that report on the thermal tolerance of fish species expressed as the critical thermal maximum (CT) or lethal thermal maximum (LT), obtained in dynamic and static assays, respectively. In addition to the thermal thresholds, we also extracted relevant information on the experimental set-up, namely the ramping rate, trial duration, starting temperature, acclimation temperature, and acclimation duration. The latitude at which the fish tested were collected was also extracted. The three existing databases supplemented with the results of the literature search yielded 3,257 upper thermal tolerance records from 565 species (Verberk et al., 2024). We classified each species into one of three groups based on information on realm (freshwater, brackish, marine) and migration obtained from FishBase and targeted internet searches: 1) fish predominantly using freshwater; this includes catadromic fish which grow up in freshwater habitats, such as eel 2) fish predominantly using marine waters; this includes anadromic fish which grow up in the ocean, such as salmonids and 3) brackish fish, which includes amphidromic fish. This classification resulted in 399 freshwater species, 219 marine species, and 48 brackish water species.

Thermal tolerance data harmonisation

Upper thermal limits of fish are quantified with different protocols. Static or LT assays expose fish to a constant temperature and note mortality after a set amount of time. The lethal temperature expresses the temperature at which the animals succumb to heat stress after the set amount of time (typically 50% mortality, but sometimes 100%). In dynamic or CT assays, the temperature that fish are exposed to is gradually ramped up and the temperature at which animals succumb is noted. However, tolerance to heat stress, like any other stressor, depends on both the stress intensity and its duration (Rezende et al., 2014). As the duration of dynamic assays varies depending on starting temperature and ramping rate, thermal thresholds recorded in CT trials are not directly comparable, and differences in duration need to be corrected for if thermal thresholds are to be compared across studies and species (Leiva et al., 2019). Therefore, we bootstrapped the data for dynamic trials 50 times, taking only a single CT value for a given species and study. Next, we combined the subset with the data from static trials and fitted a model that included the duration of the assay (in hours; log-transformed) as a fixed variable. This revealed that heat tolerance is negatively related to exposure duration (Fig S1), confirming previous work (Rezende et al., 2014; Verberk et al., 2023). We then used the fitted slope estimate (-1.26 ± 0.0135 (SD)) to standardize all the reported heat tolerances to a duration of 1 hour. Interestingly, after this standardization we no longer find a significant difference in the reported heat tolerance values between static and dynamic trials across all data ($P = 0.509$), suggesting that differences in heat tolerance between both types of trials are largely driven by differences in duration of exposure.

Thermal exposure

For each fish species, we determined the thermal regime it is exposed in its habitat as described by two key characteristics: the maximum temperature and the variability in temperature within its geographic range. To that end, we obtained geographic range maps of the species from the International Union for the Conservation of Nature (IUCN), and we overlaid these with water temperature data. For freshwater fishes, we used weekly water temperature data obtained from FutureStreams (Bosmans et al., 2022), which provides weekly water temperature data at 5 arcmin spatial resolution. Similar to Barbarossa et al. (2021), we used weekly mean values averaged over a 30-year climatology period (1976-2005), and we selected, per species, the maximum value across

the range as the maximum habitat temperature. To determine the thermal variability, we quantified the coefficient of variation across the long-term weekly mean values averages across the range. For marine and brackish fish species, we took a similar approach using data on sea surface temperature from Bio-Oracle (Assis et al., 2018).

Next, we tested for differences in thermal exposure between marine, brackish and freshwater fishes based on the 511 fish species for which we had data on latitude, maximum habitat temperature and habitat thermal variability. Since we had only a single value for maximum habitat temperature and thermal variability per species, we also subsetted the data so that we had a single value for latitude, selecting the record with median latitude when we had data spanning different latitudes. Next, we used Phylogenetic Generalized Least Squares (PGLS) to account for potential phylogenetic non-independence. We constructed separate models for maximum habitat temperature and habitat thermal variability and in each model, we also included absolute latitude as a 2nd order polynomial to account for non-linear relationships.

Thermal sensitivity

To evaluate how thermal exposure affects fish heat tolerance, we modelled heat tolerance (corrected for trial duration, see above) as a function of habitat thermal regime (habitat thermal maxima and thermal variability) or latitude (a proxy for thermal regime). To do this and account for multiple records per species, we used a Bayesian phylogenetic multilevel modelling framework, which can include both random effects due to phylogeny and due to species identity (Bürkner, 2017). We also included acclimation temperature and the interaction between thermal regime and acclimation temperature to test whether plasticity in heat tolerance is shaped by thermal conditions. We used a 2nd order polynomial for acclimation temperature to account for increasingly smaller increases in heat tolerance with increasing acclimation temperatures. Correlation plots (Fig S2) revealed that acclimation temperature was strongly correlated with maximum habitat temperature (tropical fishes are typically acclimated to higher temperatures than polar fishes). We therefore standardized acclimation temperature in two ways: relative to the maximum habitat temperature and relative to the mean acclimation temperatures for a given species. Acclimation temperature standardized relative to a species' mean acclimation temperature showed no correlation with either latitude, maximum habitat temperature or habitat thermal variability (Pearson R, $P > 0.102$) and we therefore used this standardization in further analyses.

We compared both models (model 1 based on latitude vs model 2 based on thermal regime) by calculating the marginal R^2 values and using the Pareto-smoothed importance sampling leave-one-out (PSIS-LOO) cross-validation. To test whether fishes from different realms exhibit differences in their heat tolerance and plasticity of heat tolerance, we constructed a third model based on maximum habitat temperature and thermal variability, which also included realm.

Results

Thermal exposure

Freshwater fish species experience both higher maximum temperatures and higher thermal variability in their geographic range than marine species (Fig. 1; PGLS: $t_{1,490} < 6.69$, $P < 0.001$). Brackish species also inhabit warmer habitats than marine fishes (PGLS: $t_{1,490} = 3.75$; $P < 0.001$), but the thermal variability in their geographic range does not exceed that of marine fishes (PGLS: $t_{1,438} = 1.04$; $P = 0.298$). At the median latitude, maximum habitat temperatures of freshwater fish were 3.87 °C

higher than those of marine fish (Fig. 1A), while the thermal variability was 0.0053 higher (Fig. 1C), representing a 38% increase. Thermal niches were strongly phylogenetically structured for both maximum habitat temperatures and thermal variability (lambda values of 0.820 and 0.934 respectively). Both thermal exposure metrics were strongly correlated with absolute latitude: thermal maxima were highest in the tropics (Fig. 1B), while thermal variability peaked at temperate latitudes (Fig. 1D).

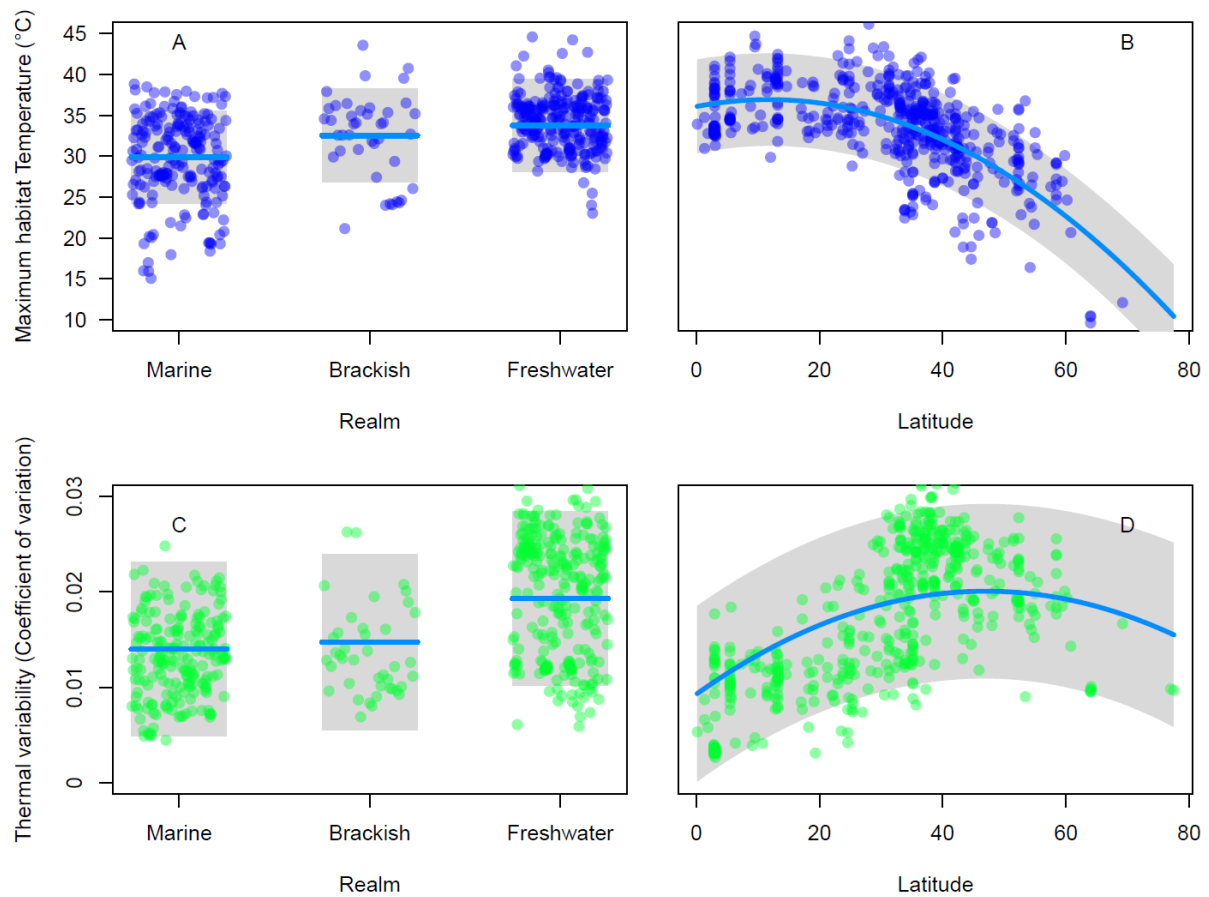


Fig 1. Partial residual plots for maximum habitat temperature (A,B), and thermal variability (C,D) for the 511 species of fishes for which we had data on habitat, latitude and thermal conditions in their distribution range. A and C show differences between fishes from marine, brackish and freshwater habitats, while B and D show the latitudinal relationships.

Thermal sensitivity

Heat tolerance of fishes varied strongly with both latitude (Fig. 2A) and thermal conditions experienced by fish in their habitat (Fig. 2B,C). In line with previous work, heat tolerance was highest in tropical fishes and declined away from the equator. However, the effect of latitude differed between the northern and southern hemispheres, which could reflect asymmetry between the two hemispheres in latitudinal variation in temperature and its variability (Chown et al., 2004). In addition, for temperate regions on the northern hemisphere (35-66.5 N) there was a large variation in heat tolerance despite a limited latitudinal range. Patterns in heat tolerance were better captured by a model based on the thermal conditions that fishes were exposed to in their habitat (partial R^2 of 55.2%), compared to models based on latitude (Partial R^2 of 36.6%). The random factors phylogeny

and species identity also explained a large part of the variation (Fig S3), resulting in total explained variation of around 90% for both models. As expected, fishes from warm habitats exhibited higher heat tolerance (Fig 1B). In addition, fishes from thermally variable habitats exhibited greater plasticity in heat tolerance (Fig. 1C), with acclimation response ratios increasing from 0.18 (when thermal variability was 0) to 0.30 (when thermal variability was 0.02).

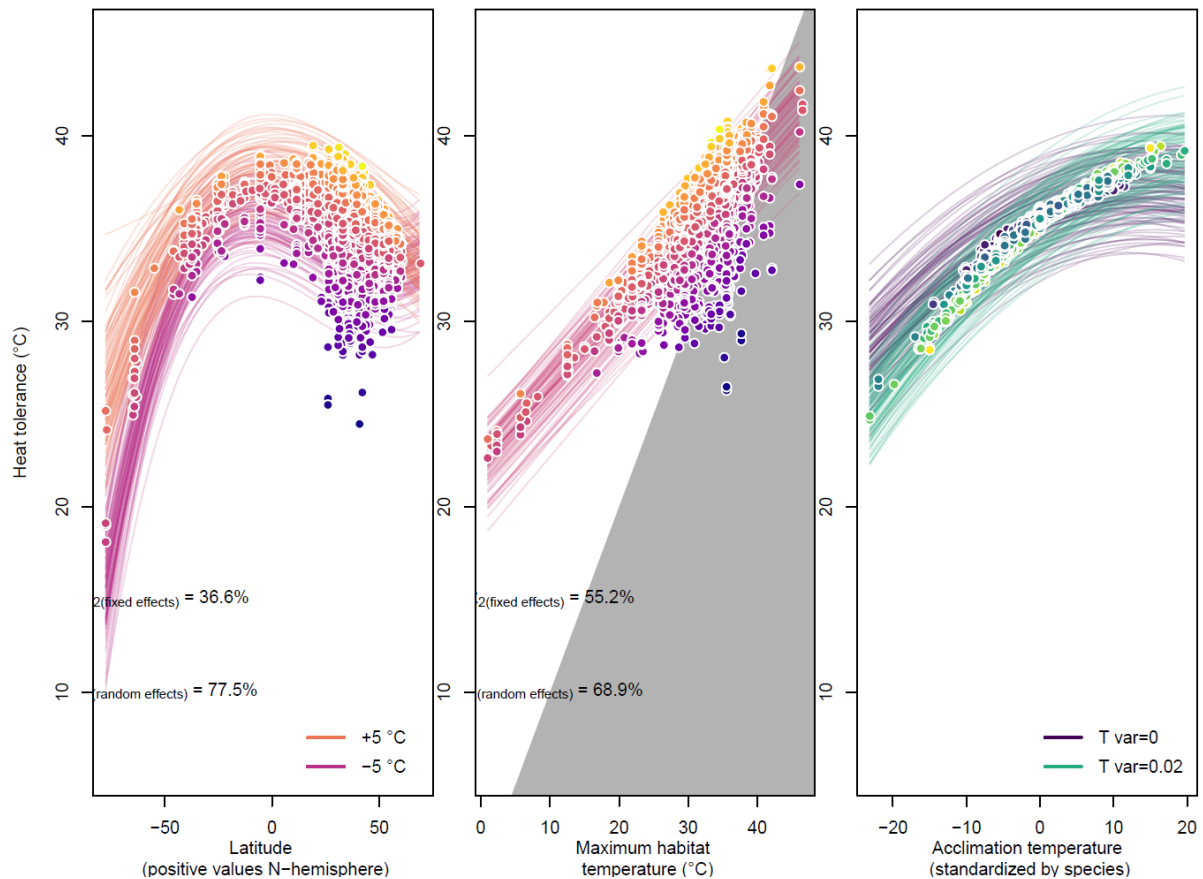


Fig 2. Heat tolerance in relation to A) latitude, for different acclimation temperatures (Table S1), B) maximum habitat temperature (Table S2), and C) acclimation temperature, for different levels of thermal variability (Table S2). The grey polygon in panel B highlights when observed heat tolerance falls below maximum habitat temperatures.

Paradoxically, several fishes were exposed to maximum habitat temperatures that exceeded their reported heat tolerance, resulting in a negative warming tolerance (i.e. heat tolerance minus maximum habitat temperature, points in the grey triangle in panel 2B). However, when we used the model based on the thermal conditions that fishes were exposed to in their habitat (Table S2) to predict the heat tolerance under the assumption that species were acclimated to this maximum habitat temperature, we no longer observed negative values for warming tolerance (Fig. 3).

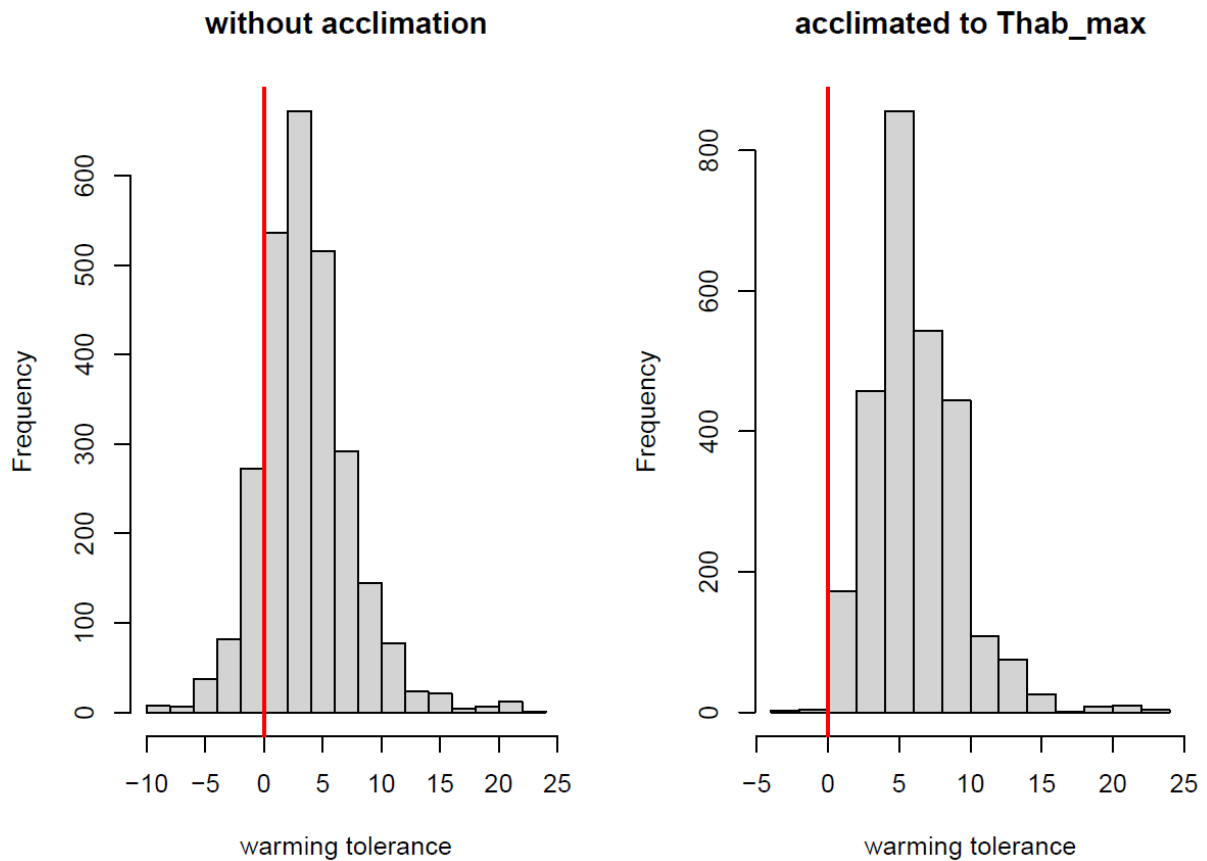


Fig 3. Frequency distribution of warming tolerance values, calculated either as (A) the reported heat tolerance minus the maximum habitat temperature, or (B) as the difference between maximum habitat temperature and the predicted heat tolerance when assuming the species is acclimated to the maximum habitat temperature.

Heat tolerance values reported for freshwater fish were higher than those for marine fish, but this reflected higher maximum habitat temperatures (Fig. 4A); after these were accounted for in the model, there was no significant difference across realms; Table S3). Plasticity in heat tolerance differs between marine and freshwater fishes (Fig. 4B,C), even when accounting for the greater thermal variability experienced by freshwater fish (Table S3), with freshwater fish being more plastic. For each degree of warm acclimation, freshwater fish initially gained on average 0.30 °C (0.299-0.332 Credible Interval) of heat tolerance, whereas marine fish gained only 0.22 °C (0.218-0.264 Credible Interval), but note that the effect of acclimation diminished according to our model because of a negative effect of the quadratic term of acclimation temperature. Fishes from brackish waters had a lower heat tolerance, and their plasticity in heat tolerance resembled that of freshwater fish.

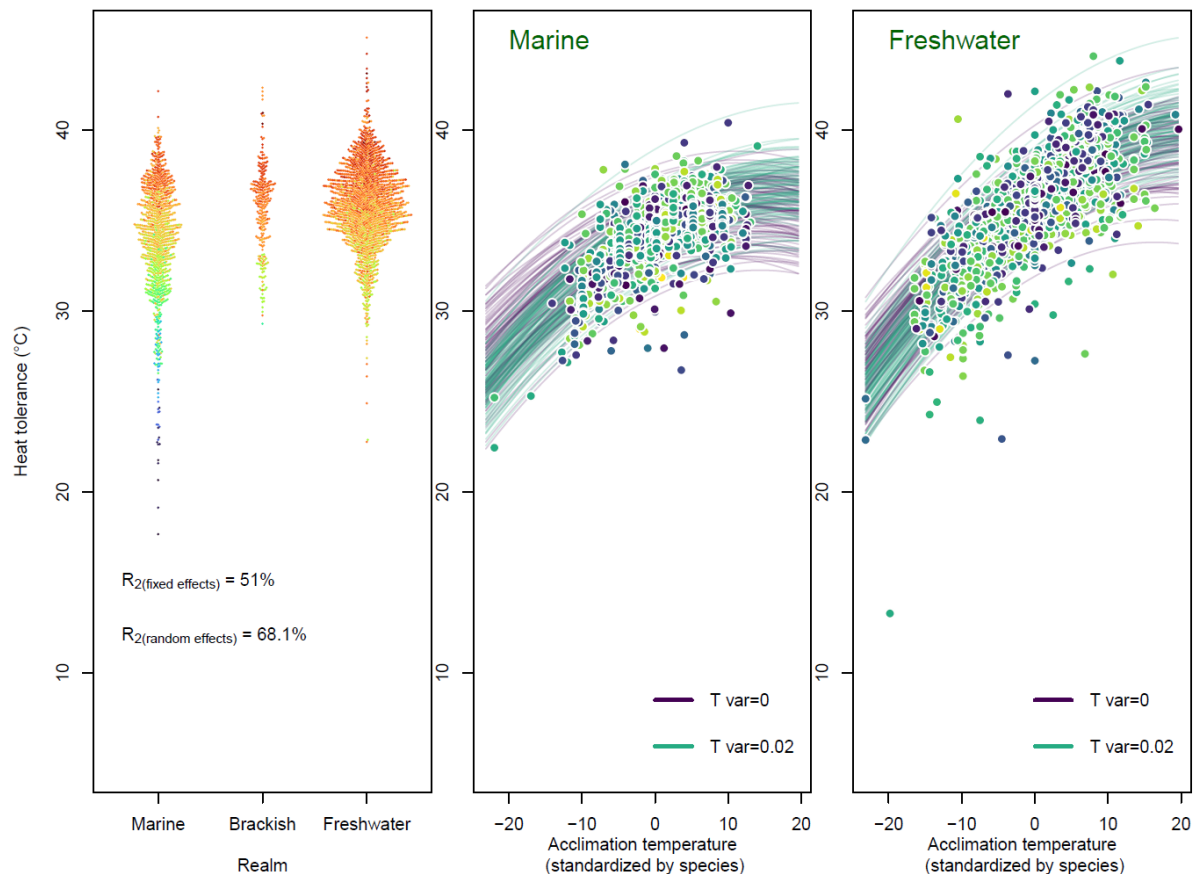


Fig 4. Reported heat tolerance values for fishes from marine, freshwater, or brackish habitats (A), with differences mainly due to differences in maximum habitat temperature (see Fig 2B, color coded from cool/blue to warm/red). Plasticity in heat tolerance is smaller in marine fishes (B) than in freshwater fishes (C).

Discussion

To effectively use ecophysiological metrics in predicting vulnerability to climate warming, these metrics must accurately represent the thermal conditions that species encountered throughout their evolutionary history. Our study demonstrates that latitudinal patterns in heat tolerance can be linked directly to geographic differences in maximum habitat temperature and thermal variability (Fig 2). We also observed a strong phylogenetic structuring, both in terms of their exposure, i.e. the thermal regime fishes experience in their habitat, and in their sensitivity, i.e. the experimentally derived tolerance values, mirroring previous work showing a strong phylogenetic structuring of heat tolerance (Bennett et al., 2021; Leiva et al., 2019).

Interestingly, in multiple instances the maximum habitat temperature exceeded the heat tolerance level of fishes. This is even more puzzling when considering that the maximum habitat temperature is based on a weekly interval, whereas the heat tolerance is corrected for a duration of 1 hour, suggesting that either that the heat tolerance reported is an underestimation, or that the habitat temperature calculated overestimates the thermal exposure experienced by species, or both. Thermal refuges such as deeper parts of a lake, or cooler sections of a stream may create refuges during heat waves. Moreover, thermal tolerance can vary seasonally, and geographically across populations so, local populations during summer may exhibit higher heat tolerance levels than

reported. This latter possibility is at least partially confirmed by our predicted heat tolerance under the assumption that all species are acclimated to their maximum habitat temperature (Fig 3).

Aquatic species are frequently juxtaposed against terrestrial species, but even within aquatic species such as fishes there is much variation in heat tolerance. Our results show that this variation is not only related to differences in habitat temperatures and variability, but we also observed greater levels of plasticity in heat tolerance in freshwater fishes than in their marine counterparts (Fig 4). This matches the observation that, compared to marine fishes, freshwater fishes are also exposed to greater thermal fluctuations (Fig 1). Previous studies have attempted to explain variation in the plasticity of heat tolerance from differences in thermal variability (Comte & Olden, 2017; Gunderson & Stillman, 2015; Seebacher et al., 2015). Our study differs in several respects. First, we used habitat thermal variability directly rather than latitude as a proxy. Second, we incorporated a large number of species that together span a large range in thermal variability experienced by drawing on freshwater and marine species. Finally, we focussed on fishes resulting in a somewhat comparable body plan across different species. Although fish as a group have a rich evolutionary history, all the species incorporated are aquatic and rely at least partly on gills to extract oxygen from the water, so variation across species is unlikely to be confounded by major differences in breathing mode.

Full thermal acclimation likely carries significant costs and constraints. If not for these costs and constraints, one would expect the evolution of perfect acclimation, i.e. an acclimatory response ratio of 1. Constraints are also reflected in the curved relationship found in our models where increases in heat tolerance are diminishing with increasing acclimation temperature. The greater plasticity of heat tolerance exhibited by freshwater fish, which live in thermally fluctuating habitat, suggests that here it is more beneficial to be plastic, rather than evolve a high basal heat tolerance.

Our findings underscore the importance of thermal physiology for predicting responses to climate change and highlight that plasticity in heat tolerance is an important mechanism to cope with thermal extremes, especially for organisms living in thermally variable habitats such as freshwater fish.

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Supplementary materials:

Table S1; Summary table of the model based on latitude

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Group-Level Effects:
~species_name (Number of levels: 499)
      Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
sd(Intercept)      2.19      0.12      1.96      2.43 1.00      5484      10644

~treename (Number of levels: 499)
      Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
sd(Intercept)      7.98      1.06      6.07     10.18 1.00      2899      5590

Population-Level Effects:
      Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
Intercept          34.75      3.19     28.44     41.08 1.00      4770      8286
polyaccT.sp21       0.07     10.07    -19.56     19.67 1.00     29605     17112
polyaccT.sp22     -16.03      2.04    -20.03    -12.06 1.00     49006     16421
accT.sp            0.29      0.03      0.23      0.36 1.00     29746     16882
polylat_collection31 -14.44      5.32    -24.92     -3.99 1.00     25396     18116
polylat_collection32 -56.49      5.37    -67.07    -45.97 1.00     13652     15800
polylat_collection33  24.97      5.05     14.98     34.83 1.00     13347     16475
accT.sp:polylat_collection31 -0.89      0.43     -1.73     -0.05 1.00     41642     17049
accT.sp:polylat_collection32 -0.07      0.47     -0.98      0.85 1.00     32891     18687
accT.sp:polylat_collection33 -3.07      0.44     -3.93     -2.19 1.00     38474     18539

Family Specific Parameters:
      Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
sigma      1.75      0.03      1.70      1.80 1.00     29686     17014

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Table S2; Summary table of the model based on habitat thermal regime

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Group-Level Effects:
~species_name (Number of levels: 499)
      Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
sd(Intercept)      2.13      0.12      1.91      2.36 1.00      5294     10383

~treename (Number of levels: 499)
      Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
sd(Intercept)      6.32      0.90      4.66      8.19 1.00      2723     5409

Population-Level Effects:
      Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
Intercept          22.43      2.70     17.18     27.83 1.00      5445     8722
polyaccT.sp21       0.01      9.89    -19.32     19.31 1.00     22393     16304
polyaccT.sp22     -15.67      2.07    -19.70    -11.60 1.00     37910     16281
accT.sp            0.18      0.04      0.11      0.26 1.00     20522     15585
Thab_cv           -16.61      9.28    -34.50      1.50 1.00     26437     17000
Thab_max           0.41      0.03      0.36      0.47 1.00      8200     12560
accT.sp:Thab_cv     5.82      0.98      3.91      7.76 1.00     33405     17120

Family Specific Parameters:
      Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
sigma      1.77      0.03      1.71      1.82 1.00     23898     16900

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Table S3; Summary table of the model based on habitat thermal regime and realm

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Group-Level Effects:
~species_name (Number of levels: 514)
  Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
sd(Intercept)      2.15      0.11      1.93      2.37 1.00      5757      10856

~treename (Number of levels: 514)
  Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
sd(Intercept)      6.33      0.89      4.69      8.16 1.00      3097      5483

Population-Level Effects:
  Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
Intercept      22.35      2.69      17.18      27.71 1.00      5988      9394
accT.sp         0.18      0.05      0.08      0.27 1.00      16608     16764
polyaccT.sp21  -0.03      9.95     -19.42     19.48 1.00      32212     16446
polyaccT.sp22  -17.39     2.03     -21.38     -13.34 1.00      41534     16388
Thab_max        0.42      0.03      0.37      0.48 1.00      9692      13732
realm_migrationBrackPamphi -0.63     0.45     -1.51      0.25 1.00      14895     15813
realm_migrationFWPcataPpota -0.29     0.42     -1.11      0.54 1.00      10843     13626
accT.sp:realm_migrationBrackPamphi -0.02     0.06     -0.15      0.10 1.00      20086     16942
accT.sp:realm_migrationFWPcataPpota 0.10     0.04      0.02      0.19 1.00      15961     16525
accT.sp:Thab_cv  3.26      2.14     -0.96      7.39 1.00      15273     15440
accT.sp:realm_migrationBrackPamphi:Thab_cv 7.16     3.62      0.09     14.24 1.00      19205     16717
accT.sp:realm_migrationFWPcataPpota:Thab_cv -0.94     2.45     -5.70      3.89 1.00      15326     15757

Family Specific Parameters:
  Estimate Est.Error l-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS
sigma      1.74      0.02      1.69      1.79 1.00      24705     16466

```

Figure S1

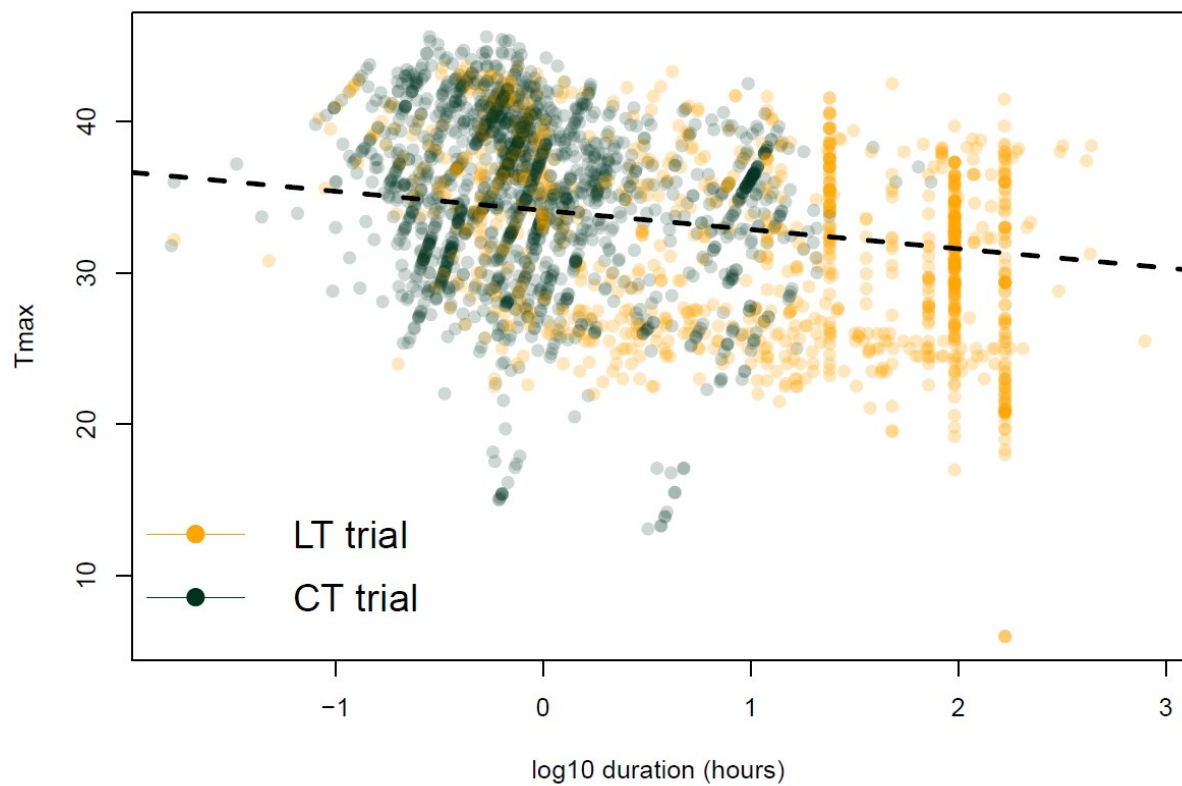


Figure S1: Effect of the duration of experimental trials to measure heat tolerance on the observed critical thermal maxima. Static trials (LT) typically have a longer duration than dynamic trials (CT).

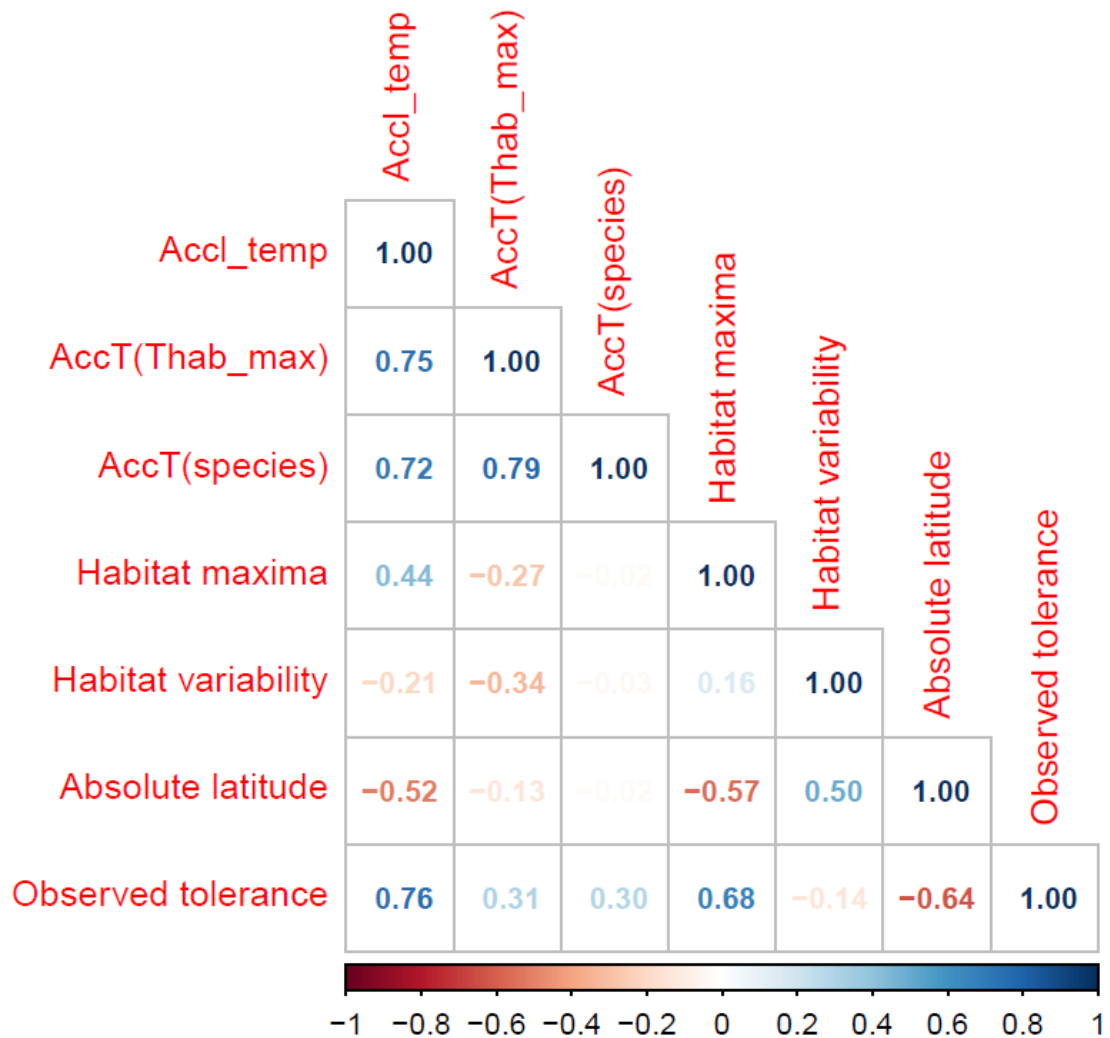


Figure S2: Correlation plot between the methodological parameter acclimation temperature (raw values and standardized by habitat temperature or species), environmental parameters (maximum habitat temperatures and thermal variability), latitude (presumed to be a proxy for these environmental parameters) and the heat tolerance observed in experimental trials.

Fig S3: Phylogeny of the species used in this study, branches and names are color coded by their observed heat tolerance.

