Thermal limits to the geographic distributions of shallow-water marine species

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Temperature profoundly affects species' geographic ranges, but the extent to which it limits contemporary range edges has been difficult to assess from laboratory experiments of thermal tolerance. The persistence of populations depends on temperature-mediated outcomes of ecological and demographic processes across all stages of a species' life history, as well as any adaptation to local temperature regimes. We assessed the relationships between sea temperature and observed distributional ranges for 1,790 shallow-water marine species from 10 animal classes and found remarkable consistencies in trends in realized thermal limits among taxa and ocean basins, as well as general agreement with previous laboratory findings. Realized thermal niches increase from the Equator towards cold-temperate locations, despite an opposite trend in geographic range size. Species' cool distribution limits are best predicted by the magnitude of seasonality within their range, while a relatively firm thermal barrier exists on the equatorward range edge for temperate species. Our findings of consistencies in realized thermal limits indicate potential limits to adaptation among common marine species and highlight the value of realized thermal niches for predicting species' distributional dynamics in warming seas.

emperature influences species' distributions through physiological and ecological processes and is one of the most important contemporary drivers of global patterns of biodiversity¹⁻⁴. Understanding how and where temperature limits species' distributions can highlight key evolutionary and biogeographic processes and is important for anticipating future biodiversity responses to a warming world^{5,6}. Establishing whether generalizable relationships exist between geographic ranges and thermal niches among species has been difficult, however, in part because temperature effects are typically confounded by numerous other interacting factors driving species distributions^{7,8}.

Our knowledge of global patterns in thermal niches of many taxa has largely come from meta-analyses of results of experiments that estimated fundamental thermal niches or thermal tolerance ranges for species exposed to extreme temperatures over short periods^{9,10}. These studies indicate that tropical (and polar) species have narrower thermal niches than temperate species^{11,12} and, for terrestrial species at least, that increasing thermal niche widths with latitude are associated with greater differences in minimum temperature limits among species than in maxima^{9,10,13}. That is, there is asymmetry in the variation of upper and lower temperature limits across species.

A prominent hypothesis explaining these patterns is that tropical species have evolved in more thermally stable environments than temperate species and thus lack natural selection for tolerance to wider temperature ranges (and particularly winter cold)^{9,14,15}. This hypothesis and its variations are often referred to as the climate variability hypothesis¹⁶. An alternative hypothesis has also recently been proposed that considers present-day species' distributions primarily as an outcome of physiology, rather than the reverse. The metabolic scaling hypothesis¹⁷ is based on the premise that physiological rates (for example, metabolic rates) ultimately influence the ecological and demographic success of species. It suggests that increasing thermal niche widths with latitude may simply reflect a near-constant range of metabolic rates across the thermal gradients, due to the scaling of rates with temperature¹⁷.

Marine species tend to have widely dispersing larvae and occupy a well-connected environment¹⁸, and their distributions may be expected to closely reflect meta-analytical findings from laboratory thermal tolerance studies⁹. Such a concordance has been noted for particular fish species for which corresponding laboratory experiments and field observations have been made^{12,19}. However, the extent to which contemporary distributions of marine species generally reflect such patterns is unknown. One anomaly in this regard is that thermal niche width is predicted to increase with increasing latitude from the Equator to cold-temperate locations, yet some crabs²⁰, molluscs²¹ and fishes²², at least, possess larger distributional spans in tropical than temperate realms.

Here, we investigate patterns in the realized thermal niche widths and geographic distributions of shallow-water marine fauna from around the world. We use data from 1,790 well-sampled mobile (that is, non-sessile) marine ectothermic species in 10 animal classes from the Reef Life Survey (RLS) database (www.reeflifesurvey. com)²³—the most comprehensive standardised global abundance database for conspicuous species associated with shallow subtidal rocky and coral reefs. We test the generality of the following predictions: (1) the realized thermal niche width of (non-polar) marine species increases with increasing latitude and decreasing environmental temperature⁹; (2) species that experience greater seasonal temperature extremes have wider thermal niches than those that live in thermally stable regions¹⁵; (3) variation in upper and lower realized thermal limits is asymmetrical, with lower limits varying more across species than upper limits9,10,24; and (4) the geographic range size of marine species decreases with increasing latitude^{20,22}.

Tropical and temperate species in shallow waters worldwide were recently found to each exhibit distributional patterns with high levels of congruency, forming two distinct 'thermal guilds', with few species possessing intermediate ranges centred in subtropical ocean climates⁶. We explicitly consider these thermal guilds when testing the above predictions, to assess whether the subtropical split in thermal affinities of the two guilds translates to differences in upper

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and lower realized thermal limits. We thus use the thermal guilds to further refine our understanding of the relationship between the temperature and geographic ranges of marine ectotherms.

We also explore species' responses to environmental gradients in latitude and temperature. Previous studies have focused on environmental gradients in latitude, but observed latitudinal differences in range size²⁵ or thermal niche widths between hemispheres and regions⁹ may simply reflect different thermal environments. Arguably, trends are more appropriately assessed in terms of environmental conditions, rather than latitude per se. We apply the thermal midpoint of species' ranges as a continuous measure of their positions within the thermal gradient.

Results

Realized thermal niches of common shallow-water marine species show remarkable consistencies across latitudinal and thermal gradients in the world's seas (Fig. 1) and largely confirm predictions based on the results of laboratory experiments; however, some nuances are evident. First, the trend for increasing niche width with latitude (and towards cooler ocean climates; prediction 1) only becomes evident when realized thermal niches consider the seasonal temperature range across occurrence locations. That is, realized niches better reflect trends from laboratory studies when they are estimated from the minimum monthly temperatures experienced by species across their distribution to the maximum monthly



Fig. 1 [Realized thermal niches as a result of latitude and sea temperature gradients. **a**-**f**, Realized thermal niches of rocky and coral reef fishes and mobile invertebrates increase along latitudinal (**a**,**b**) and sea temperature (**c**-**f**) gradients globally, as well as within temperate and tropical thermal guilds (*n*=1,790 species). The thermal niche limits in the left panels were calculated using annual mean sea temperatures from occurrence locations, whereas in the right panels they account for seasonal extremes in sea temperature across occurrence locations. Greater seasonal extremes increase the thermal niche width in higher latitudes and cooler waters (**a** and **e** compared with **b** and **f**, respectively), as well as increasing assymetry between the lower and upper limits (**c** compared with **d**). The inclusion of guilds improves the model fits in **c** and **d** from global fits for lower and upper limits (Akaike information criterion for model including 'guild' = 6,240 compared with 6,695 without 'guild' for the lower limit relationship in plot **d**, and 5,323 compared with 5,963, respectively, for the upper limits). Black lines in **a**-**d** are from generalized additive mixed-effects models, with 95% confidence intervals in grey shading. Box plots in **e**,**f** show medians (black central line) and quartiles.



Fig. 2 | Overall geographic, longitudinal and latitudinal range extents. a, The geographic range size of shallow-water marine species, measured as the extent of occurrence weighted by the density of occurrences (see Methods for calculations), decreases towards subtropical latitudes and is significantly smaller in species from temperate than tropical guilds (Supplementary Table 9). **b**,**c**, The distributions of longitudinal (**b**) and latitudinal (**c**) range extents for temperate and tropical species show that differences in the latitudinal extent contribute more than differences in the longitudinal extent to overall differences in the geographic range size. Tropical and temperate species are defined for **b** and **c** on the basis of thermal distributions, as in Fig. 1 and ref. ⁶. A general additive model has been fitted to the data in **a**, with a spline fit. Box plots show medians and quartiles.

temperatures (right panels in Fig. 1, Supplementary Tables 1–8 and Supplementary Fig. 1a), rather than when considering the thermal environment occupied by species as the range of annual mean temperatures across their distribution (left panels in Fig. 1 and Supplementary Fig. 1a). As such, accounting for seasonality in sea temperatures appears to be critical for understanding species' distribution limits in a way that reflects our understanding from laboratory studies and supports prediction 1 at the same time as providing strong support for prediction 2 (wider thermal niches in regions that experience greater seasonal extremes in temperature).

Second, thermal guilds have not previously been considered in assessing these patterns, yet an increasing realized thermal niche width towards cooler climates is clearly evident within each of the temperate and tropical guilds (Fig. 1e,f). Thus, prediction 1 is supported within thermal guilds of shallow marine species, regardless of whether seasonality is considered.

Assymetry in upper and lower limits is clear when accounting for seasonal extremes in realized thermal niches (right panels of Fig. 1), supporting prediction 3. Lower limits decrease more steeply towards cooler climates and higher latitudes than is seen for upper limits (Fig. 1d and Supplementary Tables 5 and 6). Shallow-water marine species with the widest thermal niches tend to inhabit seas with the greatest seasonal temperature extremes (prediction 2), primarily through occupying locations with cooler seasonal minima (prediction 3). This trend also occurs independently within temperate and tropical thermal guilds, although the importance of seasonality on lower limits is reduced for tropical compared with temperate species (Supplementary Figs. 2 and 3). Seasonality is still more important in describing variation in the thermal limits of species than which taxonomic class they belong to or which ocean basin they inhabit (Supplementary Fig. 2).

Prediction 4 (the geographic range size of marine species decreases with increasing latitude) is clearly supported by the shallow-water reef fauna data, with significantly larger range sizes of tropical than temperate species apparently a general pattern for these taxa when considered globally (Fig. 2). Tropical species occupy approximately twice the latitudinal range size and 1.3 times the longitudinal range size of temperate species, on average, and have considerably greater extents of occurrence (Fig. 2). This trend is consistent across classes (Table 1), although the sea stars (Asteroidea) and featherstars (Crinoidea) assessed show smaller temperate–tropical differences. The latitudinal pattern in geographic range size across all classes also suggests relatively small ranges for the few subtropical species, with dips at around 30° latitude in both hemispheres, although these and the peak in range sizes in between are offset from the Equator towards the Southern Hemisphere (Fig. 2a).

An important caveat to the use of realized thermal limits for marine species is that maximum values of the warmest-affinity tropical species are likely truncated to some extent by the maximum contemporary temperatures experienced in the world's oceans. This is most obvious when the seasonal extremes are used to estimate species' realized thermal limits (Fig. 1b,d). Using an extrapolation procedure (see Methods), we explored this truncation and estimated it to be in the order of 0.6–3.0 °C, with an estimated upper thermal limit of 34.3 °C.

Discussion

All predictions investigated here were well supported for common shallow marine fauna, which is remarkable given that these predictions were based on the outcomes of laboratory experiments and theory, and many other factors affecting species' distributions could have greatly changed the patterns of distribution from those expected on the basis of temperature alone. Thus, our results contribute further evidence that the distributions of marine ectotherms are strongly defined by contemporary sea temperatures (and temperature-dependent processes)²⁶, a phenomenon also supported by the increasing number of marine species observed shifting polewards in response to warming seas^{27–30}.

In particular, the R^2 values for linear fits through the upper and lower limits of temperate species in Fig. 1d of 0.52 and 0.83 suggest that species are occupying relatively consistent thermal ranges for any given ocean climate, with little variation in limits possibly attributable to factors other than temperature. Such other factors include inaccuracies associated with the use of satellite-derived sea temperatures and incomplete sampling of species' rangesboth of which are applicable to this study and neither of which are expected to be inconsequential. Variation between species due to dispersal potential (including larval duration and mobility), evolutionary history and biogeographic boundaries appears to be less important in determining upper and lower thermal limits to the distributions of the shallow-water marine fauna studied, unless those processes are strongly temperature dependent³¹. Taxonomic class and ocean basin may capture part of the variation associated with thermal limits as proxies for phylogeny and biogeographic variation, but these factors were of little importance in describing the realized limits in our study.

Table 1 | Mean geographic range size and realized thermal niche metrics for the marine fauna studied

Class	Temperate				Tropical			
	Species	Range (km)	TN width (°C)	RUL(°C)	Species	Range (km)	TN width (°C)	RUL(°C)
Actinopterygii	359	694	11.9	24.2	1,074	2,306	9.5	30.9
Asteroidea	42	1,011	12.9	22.2	17	2,324	10.1	30.5
Bivalvia	4	394	9.4	22.7	10	2,959	7.7	30.6
Cephalopoda	5	690	10.5	24.5				
Crinoidea	8	1,605	13.9	24.9	7	2,314	10.5	31.2
Echinoidea	27	824	13.4	23.1	25	2,584	10.1	30.3
Elasmobranchii	28	897	11.8	24.4	20	2,810	10.9	31.3
Gastropoda	70	707	11.0	23.3	41	2,320	9.4	30.8
Holothuroidea	4	981	13.6	24.9	15	3,376	10.4	30.4
Malacostraca	16	718	10.4	22.4	18	2,601	8.1	30.6

TN, thermal niche, is the measure used for Fig. 1f. RUL, realized upper thermal limit, is the 95th percentile of the thermal distribution. See Methods for further details on TN width and geographic range size calculations.

Our results, as well findings associated with connectivity between shallow marine habitats based on larval duration¹⁸, contrast with previous suggestions that ocean currents represent the primary limitation of marine species' ranges by influencing directionality and distance of dispersal³². In addition, most of the world's major marine biogeographic barriers for shallow-water marine species, including the Eastern Pacific gap and the Isthmus of Panama, tend to relate to longitudinal ranges, while latitudinal ranges (and hence thermal ranges) are typically more continuous along continental landmasses and island chains.

Intra-specific variation in thermal limits may exist in some or many of the species studied, with different populations showing local adaptation to the thermal environment, as observed for some terrestrial species³³ and an increasing number of marine species^{34,35}. Population structure probably also exists within many species' ranges due to source and sink dynamics³⁶. Realized thermal niches represent the net outcome of all intra-specific processes, however, encompassing the extremes in temperature experienced at the species level rather than the individual or population level. The relative consistency in patterns of species' thermal limits suggests firmer outer bounds to the thermal adaptation of populations at distribution limits. Thus, the future distributions of widely dispersing marine species in a warmer world should be relatively predictable based on realized thermal niches⁶. The importance of adaptive capacity for species' persistence is instead likely to be greatest for poor dispersers (including many sessile taxa), rare or range-limited species.

Our results relate to common species, which comprised 93% of individuals recorded by visual transect methods on rocky and coral reefs, on average, worldwide^{4,23}. Rarer species are perhaps more likely to be limited by dispersal or have specialized ecological needs and thus deviate from the general patterns described here. Range-restricted endemics, in particular, have high potential for dispersal limitation rather than temperature limitation of distribution²⁷. Our results do, however, cover a substantial number of range-restricted species from well-sampled hotspots of endemism, such as the Galapagos Islands (Ecuador) and Lord Howe Island (Australia), albeit only considering common species at such locations. The Galapagos and Lord Howe islands actually experience moderate seasonality in sea temperatures, and thus localized geographic ranges of species do not result in anomalously narrow thermal niche widths.

Patterns in realized thermal niches of marine species reflect the asymmetrical variation in upper and lower realized thermal limits noted from laboratory studies of terrestrial species^{10,24}. Care is

needed in interpreting trends in the asymmetry of thermal limits of tropical fauna, however, as populations of some species could potentially occur in seas warmer than the maximum monthly temperature for locations in our dataset of ~32 °C. Regardless, asymmetry is evident and clear in temperate species as well.

Different physiological processes have been proposed to affect the upper and lower thermal performance of ectotherms²⁶, with upper thermal limits suggested to show little plasticity³⁷ or evolutionary lability relative to lower limits^{10,24}. Our results notably identify and affirm the realized consequences of 'plastic floors and concrete ceilings'²⁴ in the geographic distribution of biodiversity across the world's shallow seas.

While temperature-related physiological and evolutionary processes are thought to underlie asymmetric fundamental thermal limits, some temperature-dependent ecological mechanisms could potentially also play a role in asymmetric patterns in realized limits, as studied here. If ecological pressures such as predation and competition are more intense in warmer waters as a result of increased metabolic rates or latitudinal gradients in richness and abundance^{1,4,38}, there may be an element of ecological release for populations at the cool end of species' ranges, allowing persistence even if individual performance is reduced by cooler waters. Conversely, distribution tails at the warm range edges may be shortened by more intense ecological interactions and greater densities of predators and competitors.

The Mediterranean fauna provides some support for this ecological suppression hypothesis. Species in this region have anomalously high upper thermal limits compared with other temperate species globally (the points above the upper thermal limit curve in the Northern Hemisphere in Fig. 1a,b are largely from the Mediterranean). These species experience limited overlap in distribution with a richer tropical fauna as a result of geographical isolation, although this is increasing through Lessepsian migration³⁹. Thus, speculatively, Mediterranean species can perhaps maintain viable populations in slightly warmer temperatures than observed for other temperate species, as rates of predation and competition are lower than in other locations with similar temperatures but more diverse communities.

Temperature-dependent behavioural mechanisms may also contribute to asymmetrical upper and lower limits. Persistence of species at the cool edge of their range may involve reducing activity, including through hibernation, which has been noted in many marine ectotherms⁴⁰. Hibernation appears sufficiently frequent to account for declines in observed local richness in the coolest months when habitat connectivity, mobility and emigration cannot adequately account for apparent species declines at some temperate locations $^{41-43}$.

Asymmetry in thermal limits may also partly result from biases associated with the more frequent observation of vagrant individuals at the cool range edge—the only possible direction of vagrancy for some tropical species. Poleward settlement, but not establishment, of warmer-water species is a common phenomenon in the shallow marine environment^{29,44,45}. We minimized the influence of vagrant individuals in our analysis by using the fifth percentile of thermal distributions to estimate species' lower realized thermal limits, rather than outlying records; nevertheless, our data still probably include some of these cases. Overall, regardless of the possibility of biases, the similarity between global observations and laboratory findings, and the relative consistency across taxa examined, suggests that observational biases and behavioural mechanisms are not primarily responsible for the observed asymmetrical patterns in realized thermal niches.

Our results provide a clear explanation for how contrasting latitudinal trends in thermal niche widths and range sizes of marine species occur. For tropical species, the wide equatorial band of warm ocean temperatures allows greater latitudinal expansion to larger geographic ranges relative to temperate species, without concordant increases in the thermal niche width. For temperate species, greater seasonality at higher latitudes is associated with larger thermal niche widths relative to smaller geographic range sizes. The former is not unexpected given the relatively large latitudinal distance between tropical isotherms. Tropical marine species also tend to have greater longitudinal ranges, which are probably due to the earth circumference and long width of ocean basins at low latitudes, as well as the connectivity of shallow-water habitat with similar thermal regimes through island chains and emergent coral atolls.

The pattern of increasing thermal niche width with latitude and decreasing environmental temperature was evident in the globalscale data, but more distinct within each of the two major thermal guilds when assessed separately. These guilds are not artefacts of spatial bias in sampling intensity or limitations of contemporary global and continental thermal limits (see ref.⁶ and the extended data and supplementary materials therein), but represent common geographic limits among mobile reef species, which align by temperature regardless of continent or taxonomic group. Importantly, our observation that species with distributions centred on warmtemperate waters (that is, the warmest of the temperate guild) have narrower realized thermal niche widths than those with ranges centred at only marginally lower latitudes (that is, subtropical species) deviates from expectations associated with existing hypotheses such as the climate variability hypothesis¹⁶ and the metabolic scaling hypothesis¹⁹. This pattern holds regardless of whether seasonality in temperatures is considered or not (that is, a distinct warm-temperate dip is evident in the plots of Fig. 1e,f), and is supported by better fits of linear relationships between the upper and lower limits along the temperature gradient when guilds are considered separately (as indicated by the significant interaction terms for guilds and Akaike information criterion values of competing models). An important feature is that temperate species have apparently been unable to colonize adjacent and connected warmer environments.

Although temperate and tropical marine species exhibit a clear dichotomy in thermal distributions, this has probably been previously overlooked for two reasons. First, the guilds may be features of realized thermal niches, not evident from short-term laboratory experiments that do not consider temperature-dependent processes affecting the distributions and persistence of wild populations. For example, thermal bottlenecks associated with reproduction, larval development or recruitment may exist^{46,47} such that there are common temperatures beyond which fewer species are able to maintain persistent populations.

Alternatively, the widespread use of latitude in previous studies as a proxy for thermal gradients may have hidden the distinction between temperate and tropical guilds. This appears to be the case when comparing the top and middle plots in Fig. 1, and arises due to regional variability in the thermal environment. For example, the Galapagos Islands are characterized by relatively cool waters on the Equator, resulting in a broad spread of equatorial species' lower limits in Fig. 1a,b. Likewise, differences between the Northern and Southern Hemispheres noted in laboratory studies^o, and seen in our results, likely relate to differences between realms in sea temperatures and seasonality.

The contemporary upper temperature limits of the world's tropical seas represents an important limitation for using realized thermal niches for predicting future warming-related change in the warmest seas. The distinctive patterns within guilds allowed us to make a relatively crude estimate of how much warmer the upper limits of the warmest affinity tropical species may be under warmer seas. This estimate is based on a currently untestable assumption that the same processes, whether physiological, demographic or ecological, determine variation in the upper realized limits of temperate and tropical species. This extrapolation suggests little scope for further warming (0.6-3.0°C increase in maximum temperatures) before populations of the warmest-affinity marine species are predicted to be locally extirpated. Such vulnerability of tropical marine faunas to future warming has previously been predicted⁶, including on the basis of patterns in laboratory-derived thermal tolerances⁴⁸ and modelled distributions⁴⁹.

The patterns in realized thermal niches identified here provide additional important insights for anticipating changes in marine biodiversity in the future. The common limits for temperate species (where sea temperatures reach ~25 °C in the warmest month) suggest that most temperate species in such locations may concurrently undergo warm-edge range contractions with global warming, and the extent and locations of potential mass extirpations (local extinctions) of temperate species should be predictable using climate velocity approaches^{49–51}. Many of these warm–temperate locations around the globe already receive a substantial influx of tropical species, which will continue to increase. Thus, species turnover is likely to be rapid, making spatial fisheries and conservation management more complex in these regions, including for marine protected areas and threatened species.

Methods

Thermal niche. Thermal range data were obtained from the dataset compiled for ref.⁶, which covers reef species in the RLS global dataset (www.reeflisurvey.com)²³ and additionally includes occurrence records for these species from GBIF (www.gbif.org). A confidence scoring system outlined in⁶ guided exclusion of species for which too few records were available in the combined dataset to reliably estimate thermal ranges. Thus, species included in this analysis represent common species, rather than rare species, which we consider appropriate for the goals of the study; but we acknowledge that rare species could potentially show different patterns. Polar species were also not well covered and were excluded from this analysis. These are generally considered to be highly stenothermic⁵², requiring special adaptations to live at temperatures consistently below 2 °C, and could potentially differ in the mechanisms by which temperature and geographic ranges are related.

Thermal niche width (calculated in °C) was derived through matching occurrence records to remotely sensed Sea Surface Temperature (SST) records from Bio-Oracle³³. It was calculated in two ways, both representing the range from the 5th to 95th percentile of SST records for occurrence locations of each species, but differing in which SST metrics were used. First, long-term mean annual SST data (2002–2009) were used to provide a measure of the range in average temperatures experienced by a species throughout its geographic range. Second, the 5th percentile of coolest temperatures from the temporal minimum SST from monthly climatologies across occurrence locations, and the 95th percentile of the temporal maximum SST (for details of SST data, see ref. ⁵³), were used to provide a measure of thermal niche that spanned the seasonal extremes experienced by species across its geographic range.

Geographic range. Geographic range size was calculated for each species as the latitudinal extent, longitudinal extent, and in an index of the combination of both,

weighted by the density of presence records and corrected for global variation in the linear distances represented by one degree of latitude:

 $\sqrt{(d_v \cdot \text{stdev}(\text{Lat}))^2 + (d_h \cdot \text{stdev}(\text{Long}))^2}$

Where d_v and d_h are the distances (in km) of one degree of latitude and longitude for the midpoint of a species' range, respectively, and stdev(Lat) and stdev(Long) the standard deviations of latitudes and longitudes of all occurrence locations for that species.

Statistical analyses. Linear and generalized additive mixed-effects models were used to test for relationships between thermal and geographic variables. Dependent variables comprised geographic range size and thermal niche width, and key predictors were latitudinal midpoint, thermal niche midpoint and thermal guild (temperate or tropical, based on thermal midpoint division of 23 °C, sensu⁶). Phylogeny and biogeography were also considered as mixed effects in all models, using taxonomic class as a proxy for phylogenetically-conserved effects, and ocean basin to account for the spatial structure in the data and potential differences among species that remain relatively isolated from one another.

Models involving thermal niche width were run separately for the two thermal niche width measures (annual means and seasonal extremes).

To test the relative importance of several variables (that is, thermal niche midpoint (thermal affinity), seasonality, ocean basin and class) in predicting the magnitude of the upper and lower realized thermal limits, we used random forest models, applied independently to tropical and temperate guilds. Given our variables of interest were of different types, and were correlated (thermal affinity and seasonality), we used the package 'party³⁵⁴ and the function cforest with controls = cforest unbiased, with permutation importance quantified using the function varimp with conditional = TRUE. (Supplementary Fig. 2).

Extrapolation of contemporary upper thermal limits. The warmest realized thermal limits for tropical species are currently limited to the warmest temperatures experienced in the world's oceans. To explore the potential magnitude of truncation and estimate potential upper realized thermal limits of shallow-water marine species in the absence of a contemporary ocean temperature ceiling, we used the linear slope of the upper thermal limits of species in the temperate guild with environmental temperature (from Fig. 1d). We extrapolated the trend for the tropical guild, anchoring the intercept by the 'cooler' tropical species (i.e. those with lowest upper thermal limit values, which are not limited by contemporary maximum sea temperatures). This method assumes that the same limiting processes operate on upper limits of species in tropical and temperate guilds. This assumption is presently impossible to evaluate, and our estimate of a potential maximum warm limit for the warmest-affinity species in the dataset is therefore speculative. Temperate species are generally not constrained in upper limits by geography, with well-connected north-south coastlines of most continents typically not preventing shallow temperate reef species from inhabiting warmer waters than they currently inhabit.

Data availability. All data underlying analyses in this paper are publically available. The fish data are described in ref.²³ and a 'live' version of all RLS data that is continually updated is accessible through http://reeflifesurvey.com (archived versions are also available via www.gbif.org).

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Author contributions

R.D.S.-S. and A.E.B. conceived the idea. G.J.E. and R.D.S.-S. assisted with data collection. R.D.S.-S. drafted the manuscript with contributions from A.E.B. and G.J.E. A.E.B. performed the data analysis and prepared the plots.

Competing interests

The authors declare no competing financial interests.

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