https://www.nature.com/articles/s41559-017-0353-x PRE-PRINT

Thermal limits to the geographic distributions of shallow marine species

Rick D. Stuart-Smith[1]*, Graham J. Edgar[1], Amanda E. Bates[2]

[1]Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania, 7001 Australia

[2]Ocean and Earth Science, National Oceanography Centre Southampton, University of Southampton, Southampton, SO14 3ZH UK

*Corresponding author. email: rstuarts@utas.edu.au

https://www.nespmarine.edu.au/document/thermal-limits-geographic-distributions-shallow-water-marine-species

SUMMARY

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. 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 assess relationships between sea temperature and observed distributional ranges for 1,790 shallow water marine species from 10 animal classes, and find remarkable consistencies in trends in realised thermal limits among taxa and ocean basins, and general agreement with previous laboratory findings. Realised 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 realised thermal limits indicate potential limits to adaptation among common marine species, and highlight the value of realised thermal niches for predicting species' distributional dynamics in warming seas.

Keywords: Fundamental thermal niche, realised niche, thermal tolerance, biogeography, geographic range, climate change

Main text

Temperature influences species' distributions through physiological and ecological processes, and is one of the most important contemporary drivers of global patterns of biodiversity[1-4]. 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 generalisable 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 niche or thermal tolerance range 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 width with latitude is associated with greater differences in minimum temperature limits among species than in maxima[9,10,13]. That is, there is asymmetry in 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 Hypothesis[16]. An alternative hypothesis has also recently been proposed which considers present-day species' distributions primarily as an outcome of physiology, rather than the reverse. The Metabolic Scaling Hypothesis[17] is based on the premise that physiological rates (e.g. 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 temperature[17].

Marine species tend to have widely dispersing larvae and occupy a well-connected environment[18], and their distributions may be expected to closely reflect meta-analytical findings from laboratory thermal tolerance studies[9]. Such a concordance has been noted for particular fish species for which corresponding laboratory experiments and field observations have been made[12,19]. The extent to which contemporary distributions of marine species generally reflect such patterns is unknown, however. One anomaly in this regard is that thermal niche width is predicted to increase with increasing latitude from the equator to cool temperate locations, yet some crabs[20], molluscs[21] and fishes[22], at least, possess larger distributional spans in tropical than temperate realms.

Here we investigate patterns in the realised thermal niche widths and geographic distributions of shallow water marine fauna from around the world. We use data from 1,790 well-sampled mobile (i.e. non-sessile) marine ectothermic species in 10 animal classes from the Reef Life Survey 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 realised thermal niche width of (non-polar) marine species increases with increasing latitude and decreasing environmental temperature[9],
2. Species that experience greater seasonal temperature extremes have wider thermal niches than those that live in thermally stable regions[15],
3. Variation in upper and lower realised thermal limits is asymmetrical, with lower limits varying more across species than upper limits[9,10,24], and
4. 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 climates[6]. 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 and lower realised thermal limits. We thus use the thermal guilds to further refine our understanding of the relationship between temperature and geographic ranges of marine ectotherms.

We also explore species' responses to environmental gradients in latitude and temperature. Previous studies have focussed on the former, but observed latitudinal differences in range size[25] or thermal niche widths between hemispheres and regions[9] 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

Realised 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 results of laboratory experiments; however, some nuances are evident. Firstly, the trend for increasing niche width with latitude (and towards cooler ocean climates; Prediction 1) only becomes evident when realised thermal niches consider the seasonal temperature range across occurrence locations. That is, realised 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 temperatures (Fig. 1, right panels; Supplementary Tables 1-8; Supplementary Fig. 1a), rather than when considering the thermal environment occupied by species as the range of annual mean temperatures across their distribution (Fig. 1 left panels, Supplementary Fig. 1a). As such, accounting for seasonality in sea temperatures appears 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).

Secondly, thermal guilds have not previously been considered in assessing these patterns, yet an increasing realised 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 realised thermal niches (right panels of Fig 1), supporting Prediction 3. Lower limits decrease more steeply towards cooler climates and higher latitudes than is seen in upper limits (Fig. 1d; Supplementary Tables 5 & 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 to temperate species (Supplementary Fig. 2; Supplementary Fig. 3). Seasonality is still more important in describing variation in thermal limits of species than which taxonomic class they belong to, or which ocean basin they inhabit (Supplementary Fig. 2).

Prediction 4 (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 degrees 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 realised 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 in estimation of species' realised 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 outcomes of laboratory experiments and physiological theory, and many other factors affecting species' distributions could have greatly changed 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], adding to support provided by the increasing number of marine species observed shifting polewards in response to warming seas[27-30].

In particular, the R^2 for linear fits through 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' ranges – both applicable to this study, and neither expected to be inconsequential. Variation between species due to dispersal potential (including larval duration and mobility), evolutionary history, and biogeographic boundaries appear 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-dependent[31]. 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 realised limits in our study.

Our results, as well findings associated with connectivity between shallow marine habitats based on larval duration[18], contrast previous suggestions that ocean currents represent the primary limitation of marine species' ranges through influencing directionality and distance of dispersal[32]. 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 species[33] and an increasing number of marine species[34,35]. Population structure probably also exists within many species' ranges due to source and sink dynamics[36]. Realised 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 suggest firmer outer bounds to 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 realised thermal niches[6]. 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 specialised ecological needs, and thus deviate from general patterns described here. Range-restricted endemics, in particular, have high potential for dispersal-limitation rather than temperature limitation of distribution[27]. 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. Galapagos and Lord Howe Island actually experience moderate seasonality in sea temperatures, and thus localised geographic ranges of species do not result in anomalously narrow thermal niche widths.

Patterns in realised thermal niches of marine species reflect the asymmetrical variation in upper and lower realised thermal limits noted from laboratory studies of terrestrial species[10,24]. Care is needed in interpreting trends in asymmetry of thermal limits of the 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 also.

Differences in physiological processes have been proposed to affect upper and lower thermal performance of ectotherms[26], with upper thermal limits suggested to show little plasticity[37] or evolutionary lability relative to lower limits[10,24]. Our results notably identify and affirm the realised 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 realised 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. 2a,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 migration[39]. Thus, speculatively, Mediterranean species can perhaps maintain viable populations in slightly warmer temperatures than observed for other temperate species, because rates of predation and competition are lower than other locations with similar temperatures but more co-occurring species.

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 ectotherms[40]. 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 minimised the influence of vagrant individuals in our analysis by using the fifth percentile of thermal distributions to estimate species' lower realised thermal limits, rather than outlying records; nevertheless, our data still possibly reflect some of these cases. Overall, regardless of the possibility of biases, the similarity between global observations and laboratory findings, and relative consistency across taxa examined, suggests that observational biases and behavioural mechanisms are not primarily responsible for the observed asymmetrical patterns in realised thermal niche.

Our results provided a clear explanation for how contrasting latitudinal trends in thermal niche width 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 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 full earth circumference and long width of ocean basins at low latitudes, and 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 global-scale data, but was 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[6] and 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 warm-temperate waters (i.e. the warmest of the temperate guild) have narrower realised thermal niche widths than those with ranges centred at only marginally lower latitudes (i.e. subtropical species) deviates from expectations associated with existing hypotheses such as the Climate Variability Hypothesis[16] and the Metabolic Scaling Hypothesis[19]. This pattern holds regardless of whether seasonality in temperatures is considered or not (i.e. a distinct warm-temperate dip is evident in both plots e and f of Fig. 1), and is supported by better fits of linear relationships between upper and lower limits along the temperature gradient when guilds are considered separately (as indicated by significant interaction terms for guilds, and AIC values of competing models). An important feature is that temperate species have apparently been unable to colonise 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. Firstly, the guilds may be features of realised 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 our Fig. 1, and arises due to regional variability in the thermal environment. For example, the Galapagos Islands are characterised by relatively cool waters on the equator, resulting in a broad spread of equatorial species' lower limits in Fig. 1a, b. Likewise, differences between Northern and Southern Hemispheres noted in laboratory studies[9], and seen in our results, likely relate to differences between realms in sea temperatures and seasonality.

The contemporary upper sea temperature limits of in the world's tropical oceans represents an important limitation for using realised thermal niches for predicting 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 upper realised 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 predicted[6], including on the basis of patterns in laboratory-derived thermal tolerances[48] and modelled distributions[49].

The patterns in realised thermal niches identified here provide additional important insights for anticipating changes in marine biodiversity through 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[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 in[6] 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 stenothermic[52], 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-Oracle[53]. 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[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:

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

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 Generalised 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, *sensu*[6]). 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 (i.e., thermal niche midpoint (thermal affinity), seasonality, ocean basin and class) in predicting the magnitude of the upper and lower realised 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 "party"[54] 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 realised 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 realised 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.

REFERENCES

1 Tittensor, D. P. *et al.* Global patterns and predictors of marine biodiversity across taxa. *Nature* **466**, 1098-1101 (2010).

2 Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B. & Thomas, C. D. Rapid Range Shifts of Species Associated with High Levels of Climate Warming. *Science* **333**, 1024-1026, doi:10.1126/science.1206432 (2011).

3 Woodward, F. I. *Climate and plant distribution*. (Cambridge University Press, 1987).

4 Edgar, G. *et al.* Abundance and local-scale processes contribute to multi-phyla gradients in global marine diversity. *Science Advances* **in press** (2017).

5 Lee-Yaw, J. A. *et al.* A synthesis of transplant experiments and ecological niche models suggests that range limits are often niche limits. *Ecol. Lett.* **19**, 710-722, doi:10.1111/ele.12604 (2016).

6 Stuart-Smith, R. D., Edgar, G. J., Barrett, N. S., Kininmonth, S. J. & Bates, A. E. Thermal biases and vulnerability to warming in the world's marine fauna. *Nature* **528**, 88-92, doi:10.1038/nature16144 (2015).

7 Gaston, K. J. & Fuller, R. A. The sizes of species' geographic ranges. *J. Appl. Ecol.* **46**, 1-9, doi:10.1111/j.1365-2664.2008.01596.x (2009).

8 Sexton, J. P., McIntyre, P. J., Angert, A. L. & Rice, K. J. Evolution and Ecology of Species Range Limits. *Annu. Rev. Ecol., Evol. Syst.* **40**, 415-436, doi:10.1146/annurev.ecolsys.110308.120317 (2009).

9 Sunday, J. M., Bates, A. E. & Dulvy, N. K. Global analysis of thermal tolerance and latitude in ectotherms. *Proceedings of the Royal Society B: Biological Sciences* **278**, 1823-1830, doi:10.1098/rspb.2010.1295 (2011).

10 Araújo, M. B. *et al.* Heat freezes niche evolution. *Ecol. Lett.* **16**, 1206-1219, doi:10.1111/ele.12155 (2013).

11 Pörtner, H. O. & Farrell, A. P. Physiology and Climate Change. *Science* **322**, 690-692, doi:10.1126/science.1163156 (2008).

12 Pörtner, H. Climate change and temperature-dependent biogeography: oxygen limitation of thermal tolerance in animals. *Naturwissenschaften* **88**, 137-146, doi:10.1007/s001140100216 (2001).

13 Addo-Bediako, A., Chown, S. L. & Gaston, K. J. Thermal tolerance, climatic variability and latitude. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **267**, 739-745, doi:10.1098/rspb.2000.1065 (2000).

14 Tewksbury, J. J., Huey, R. B. & Deutsch, C. A. Putting the Heat on Tropical Animals. *Science* **320**, 1296-1297, doi:10.1126/science.1159328 (2008).

15 Janzen, D. H. Why Mountain Passes are Higher in the Tropics. *The American Naturalist* **101**, 233-249, doi:doi:10.1086/282487 (1967).

16 Stevens, G. C. The latitudinal gradient in geographical range: how so many species coexist in the tropics. *Am. Nat.*, 240-256 (1989).

17 Payne, N. L. & Smith, J. A. An alternative explanation for global trends in thermal tolerance. *Ecol. Lett.* **20**, 70-77, doi:10.1111/ele.12707 (2017).

18 Mora, C. *et al.* High connectivity among habitats precludes the relationship between dispersal and range size in tropical reef fishes. *Ecography* **35**, 89-96, doi:10.1111/j.1600-0587.2011.06874.x (2012).

19 Payne, N. L. *et al.* Temperature dependence of fish performance in the wild: links with species biogeography and physiological thermal tolerance. *Funct. Ecol.* **30**, 903-912, doi:10.1111/1365-2435.12618 (2016).

20 Papacostas, K. J. & Freestone, A. L. Latitudinal gradient in niche breadth of brachyuran crabs. *Global Ecol. Biogeogr.* **25**, 207-217, doi:10.1111/geb.12400 (2016).

21 Roy, K., Jablonski, D. & Valentine, J. W. Eastern Pacific molluscan provinces and latitudinal diversity gradient: no evidence for "Rapoport's rule". *Proceedings of the National Academy of Sciences* **91**, 8871-8874 (1994).

22 Rohde, K., Heap, M. & Heap, D. Rapoport's rule does not apply to marine teleosts and cannot explain latitudinal gradients in species richness. *Am. Nat.* **142**, 1-16 (1993).

23 Edgar, G. J. & Stuart-Smith, R. D. Systematic global assessment of reef fish communities by the Reef Life Survey program. *Scientific Data* **1**, 140007, doi:10.1038/sdata.2014.7 (2014).

24 Sandblom, E. *et al.* Physiological constraints to climate warming in fish follow principles of plastic floors and concrete ceilings. *Nat Commun* **7**, doi:10.1038/ncomms11447 (2016).

25 Gaston, K. J., Blackburn, T. M. & Spicer, J. I. Rapoport's rule: time for an epitaph? *Trends in Ecology and Evolution* **13**, 70-74 (1998).

26 Pörtner, H. O. Climate variations and the physiological basis of temperature dependent biogeography: systemic to molecular hierarchy of thermal tolerance in animals. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* **132**, 739-761, doi:http://dx.doi.org/10.1016/S1095-6433(02)00045-4 (2002).

27 Sunday, J. M. *et al.* Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. *Ecol. Lett.* **18**, 944-953, doi:10.1111/ele.12474 (2015).

28 Poloczanska, E. S. *et al.* Global imprint of climate change on marine life. *Nature Clim. Change* **3**, 919-925, doi:10.1038/nclimate1958

http://www.nature.com/nclimate/journal/v3/n10/abs/nclimate1958.html#supplementary-information (2013).

29 Figueira, W. F., Biro, P., Booth, D. J. & Valenzuela, V. C. Performance of tropical fish recruiting to temperate habitats: Role of ambient temperature and implications of climate change. *Mar. Ecol. Prog. Ser.* **384**, 231-239 (2009).

30 Last, P. R. *et al.* Long-term shifts in abundance and distribution of a temperate fish fauna: a response to climate change and fishing practices. *Global Ecol. Biogeogr.* **20**, 58–72 (2011).

31 O'Connor, M. I. *et al.* Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *Proceedings of the National Academy of Sciences* **104**, 1266-1271, doi:10.1073/pnas.0603422104 (2007).

32 Gaylord, B., Gaines, S. D. & Associate Editor: Hugh, P. Temperature or Transport? Range Limits in Marine Species Mediated Solely by Flow. *The American Naturalist* **155**, 769-789, doi:10.1086/303357 (2000).

33 Angert, A. L., Sheth, S. N. & Paul, J. R. Incorporating Population-Level Variation in Thermal Performance into Predictions of Geographic Range Shifts. *Integr. Comp. Biol.* **51**, 733-750, doi:10.1093/icb/icr048 (2011).

34 Bennett, S., Wernberg, T., Arackal Joy, B., de Bettignies, T. & Campbell, A. H. Central and rear-edge populations can be equally vulnerable to warming. *Nat Commun* **6**, 10280, doi:10.1038/ncomms10280 (2015).

35 Sanford, E. & Kelly, M. W. Local Adaptation in Marine Invertebrates. *Annual Review of Marine Science* **3**, 509-535, doi:10.1146/annurev-marine-120709-142756 (2011).

36 Pulliam, H. R. Sources, Sinks, and Population Regulation. *The American Naturalist* **132**, 652-661, doi:doi:10.1086/284880 (1988).

37 Gunderson, A. R. & Stillman, J. H. Plasticity in thermal tolerance has limited potential to buffer ectotherms from global warming. *Proceedings of the Royal Society B: Biological Sciences* **282**, doi:10.1098/rspb.2015.0401 (2015).

38 Stuart-Smith, R. D. *et al.* Integrating abundance and functional traits reveals new global hotspots of fish diversity. *Nature* **501**, 539-542, doi:10.1038/nature12529 (2013).

39 Spanier, E. & Galil, B. S. Lessepsian migration: a continuous biogeographical process. *Endeavour* **15**, 102-106, doi:http://dx.doi.org/10.1016/0160-9327(91)90152-2 (1991).

40 Campbell, H. A., Fraser, K. P. P., Bishop, C. M., Peck, L. S. & Egginton, S. Hibernation in an Antarctic Fish: On Ice for Winter. *PLOS ONE* **3**, e1743, doi:10.1371/journal.pone.0001743 (2008).

41 Masuda, R. Seasonal and interannual variation of subtidal fish assemblages in Wakasa Bay with reference to the warming trend in the Sea of Japan. *Environ. Biol. Fishes* **82**, 387-399, doi:10.1007/s10641-007-9300-z (2008).

42 Edgar, G. J. & Barrett, N. S. Effects of the declaration of marine reserves on Tasmanian reef fishes, invertebrates and plants. *J. Exp. Mar. Biol. Ecol.* **242**, 107-144 (1999).

43 Costello, M. J., Darwall, W. R. & Lysaght, S. in *Biology and Ecology of Shallow Coastal Waters: Proceedings of the 28th European Marine Biology Symposium, Institute of Marine Biology of Crete.* (Environmental Sciences Unit, Trinity College, University of Dublin, Dublin 2, Ireland).

44 Bates, A. E. *et al.* Defining and observing stages of climate-mediated range shifts in marine systems. *Global Environ. Change* **26**, 27-38, doi:http://dx.doi.org/10.1016/j.gloenvcha.2014.03.009 (2014).

45 Booth, D. J., Figueira, W. F., Gregson, M. A., Brown, L. & Beretta, G. Occurrence of tropical fishes in temperate southeastern Australia: Role of the East Australian Current. *Estuar. Coast. Shelf Sci.* **72**, 102-114 (2007).

46 Orton, J. H. Sea-Temperature, Breeding and Distribution in Marine Animals. *J. Mar. Biol. Assoc. India* **12**, 339-366 (1920).

47 Hutchins, L. W. The Bases for Temperature Zonation in Geographical Distribution. *Ecol. Monogr.* **17**, 325-335, doi:10.2307/1948663 (1947).

48 Comte, L. & Olden, J. D. Climatic vulnerability of the world[rsquor]s freshwater and marine fishes. *Nature Clim. Change* **advance online publication**, doi:10.1038/nclimate3382

http://www.nature.com/nclimate/journal/vaop/ncurrent/abs/nclimate3382.html#supplementary-information (2017).

49 García Molinos, J. *et al.* Climate velocity and the future global redistribution of marine biodiversity. *Nature Clim. Change* **advance online publication**, doi:10.1038/nclimate2769

http://www.nature.com/nclimate/journal/vaop/ncurrent/abs/nclimate2769.html#supplementary-information (2015).

50 Burrows, M. T. *et al.* Geographical limits to species-range shifts are suggested by climate velocity. *Nature* **507**, 492-495, doi:10.1038/nature12976 (2014).

51 Burrows, M. T. *et al.* The pace of shifting climate in marine and terrestrial ecosystems. *Science* **334**, 652-655, doi:10.1126/science.1210288 (2011).

52 Peck, L. S. & Conway, L. Z. The myth of metabolic cold adaptation: oxygen consumption in stenothermal Antarctic bivalves. *Geological Society, London, Special Publications* **177**, 441-450, doi:10.1144/gsl.sp.2000.177.01.29 (2000).

53 Tyberghein, L. *et al.* Bio-ORACLE: a global environmental dataset for marine species distribution modelling. *Global Ecol. Biogeogr.* **21**, 272-281, doi:10.1111/j.1466-8238.2011.00656.x (2012).

54 Strobl, C., Boulesteix, A.-L., Kneib, T., Augustin, T. & Zeileis, A. Conditional variable importance for random forests. *BMC Bioinformatics* **9**, 307 (2008).

ACKNOWLEDGEMENTS

We thank the many Reef Life Survey (RLS) divers who participated in collection of the data used in the analyses and provide ongoing expertise and commitment to the program, University of Tasmania staff including Antonia Cooper, Just Berkhout, Marlene Davey, Justin Hulls, Elizabeth Oh, Ella Clausius and Jemina Stuart-Smith. Development of RLS was supported by the former Commonwealth Environment Research Facilities Program, while analyses were supported by the Marine Biodiversity Hub, a collaborative partnership supported through the Australian Government's National Environmental Science Programme (NESP) and by the Australian Research Council. Additional funding and support for RLS field surveys was provided by grants from The Ian Potter Foundation and Parks Australia.

Authorship contributions: RSS and AEB conceived the idea; GJE, RSS and many others collected the data; RSS drafted the manuscript with contributions from AEB and GJE; AEB undertook data analysis and prepared plots.

Competing financial interests

The authors declare no competing financial interests.

Data Availability

All data underlying analyses in this paper are publically-available. The fish data were described in [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).

FIGURE LEGENDS

Figure 1. Realised thermal niches of rocky and coral reef fishes and mobile invertebrates increase along latitudinal (a, b) and sea temperature (c, d, e, f) gradients globally, as well as within temperate and tropical thermal guilds (*n* = 1,790 species). Thermal niche limits in left panels are calculated using annual mean sea temperatures from occurrence locations, while in the right panels they account for seasonal extremes in sea temperature across occurrence locations. Greater seasonal extremes increase thermal niche width in higher latitudes and cooler waters (plots a and e compared to plots b and f, respectively), as well as increasing assymetry between lower and upper limits (plot c compared to d). Inclusion of guilds improves model fits in plots (c) and (d) from global fits for lower

and upper limits (AIC for model including “guild” = 6240 *cf* 6695 without “guild” for the lower limit relationship in plot d, and 5323 *cf* 5963, respectively for the upper limits).

Figure 2. Geographic range size of shallow water marine species, measured as the extent of occurrence weighted by the density of occurrences (a; see Methods for calculations), decreases towards subtropical latitudes and is significantly smaller in species from temperate than tropical guilds (Table S9). The distribution of longitudinal (b) and latitudinal (c) range extents for temperate and tropical species show that differences in latitudinal extent contribute more than in longitudinal extent to overall differences in geographic range size. Tropical and temperate species are defined for (b) and (c) on the basis of thermal distributions, as in Fig. 1 and in[6]. A General Additive Model has been fitted to the data in plot (a), with a spline fit. Box plots show median and quartiles.

TABLES

Table 1. Number of species assessed, mean geographic range size (km), mean realised thermal niche width (TN width) (°C), and mean realised upper thermal limits (RUL) (°C of the 95th percentile of thermal distribution) for shallow water marine fauna studied. The thermal niche width measure used was the same as for Fig. 1f, described in methods (as is calculation of geographic range size).

	Temperate				**Tropical**			
class	**Species**	**Range**	**TN width**	**RUL**	**Species**	**Range**	**TN width**	**RUL**
Actinopterygii	359	694	11.9	24.2	1074	2306	9.5	30.9

Asteroidea	42	1011	12.9	22.2	17	2324	10.1	30.5
Bivalvia	4	394	9.4	22.7	10	2959	7.7	30.6
Cephalopoda	5	690	10.5	24.5				
Crinoidea	8	1605	13.9	24.9	7	2314	10.5	31.2
Echinoidea	27	824	13.4	23.1	25	2584	10.1	30.3
Elasmobranchii	28	897	11.8	24.4	20	2810	10.9	31.3
Gastropoda	70	707	11.0	23.3	41	2320	9.4	30.8
Holothuroidea	4	981	13.6	24.9	15	3376	10.4	30.4
Malacostraca	16	718	10.4	22.4	18	2601	8.1	30.6