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Climate change threatens the world's marine protected areas

John F. Bruno[1*], Amanda E. Bates[2,3], Chris Cacciapaglia[4], Elizabeth P. Pike[5], Steven C. Amstrup[6,7], Ruben van Hooidonk[8,9], Stephanie A. Henson[10] and Richard B. Aronson[4]

Marine protected areas (MPAs) are a primary management tool for mitigating threats to marine biodiversity[1,2]. MPAs and the species they protect, however, are increasingly being impacted by climate change. Here we show that, despite local protections, the warming associated with continued business-as-usual emissions (RCP8.5)[3] will likely result in further habitat and species losses throughout low-latitude and tropical MPAs[4,5]. With continued business-as-usual emissions, mean sea-surface temperatures within MPAs are projected to increase 0.035 °C per year and warm an additional 2.8 °C by 2100. Under these conditions, the time of emergence (the year when sea-surface temperature and oxygen concentration exceed natural variability) is mid-century in 42% of 309 no-take marine reserves. Moreover, projected warming rates and the existing 'community thermal safety margin' (the inherent buffer against warming based on the thermal sensitivity of constituent species) both vary among ecoregions and with latitude. The community thermal safety margin will be exceeded by 2050 in the tropics and by 2150 for many higher latitude MPAs. Importantly, the spatial distribution of emergence is stressor-specific. Hence, rearranging MPAs to minimize exposure to one stressor could well increase exposure to another. Continued business-as-usual emissions will likely disrupt many marine ecosystems, reducing the benefits of MPAs.

Species largely restricted to marine reserves could be especially sensitive to anthropogenic climate change because of their typically small populations and low genetic diversities[6]. Case studies indicate that global-warming-induced climate changes are already having substantial effects on populations and ecosystems otherwise protected within terrestrial and marine reserves[7,8]. Gradual warming over the past several decades and unusually high seawater temperatures in early 2016, for example, caused mass coral mortality across much of the northern Great Barrier Reef (GBR), a UNESCO World Heritage Site and model MPA[9]. Despite its isolation and effective protection from harvesting, pollution, and other stressors, warming radically altered the northern GBR. This and similar case studies, as well as synthetic analysis[10], call into question the long-term effectiveness of MPAs in protecting their resident biotas in the face of climate change.

Anthropogenic carbon emissions lead to acute and chronic perturbations, including increasing storm intensity, rising sea levels, altered upwelling regimes, ocean acidification and deoxygenation[11–14]. As a result, organisms must simultaneously adjust their physiologies to cope with multiple threats that in some cases could be selecting for opposing traits. We focused on two critical effects influencing MPAs: rising temperatures and changing oxygen concentrations. The oceans are absorbing more than 90% of the additional heat trapped by anthropogenic greenhouse gases, causing increases in ocean temperature even in the deep sea[15]. Deoxygenation, caused by warming and increasing shallow-water stratification, is predicted to affect primary production and a variety of physiological and geochemical processes[13,16]. Moreover, warming and deoxygenation can impact organisms synergistically because warming decreases oxygen concentration while increasing the metabolism and oxygen demand of ectotherms—for example, fishes and invertebrates[17].

We asked how much the world's MPAs can be expected to warm and lose oxygen under the business-as-usual (BAU) emissions trajectory RCP8.5 and the RCP4.5 mitigation scenario, for which emissions peak around 2040 and the CO_2 concentration stabilizes at ~525 ppm in 2100[2]. We used CMIP5 models to predict the mean twenty-first century rate of change in sea-surface temperature (SST) and O_2 at the geographic centres of 8,236 MPAs around the world (Fig. 1a). We also assessed warming and deoxygenation rates in 309 no-take reserves (a subset of the 8,236 MPAs), in which fishing is banned.

With BAU emissions, mean SSTs are predicted to increase within nearly all MPAs: the average warming rate is 0.035 °C year^{-1} (Table 1), with a maximum increase of 0.113 °C year^{-1} in northern Baffin Bay off northwest Greenland. This predicted future warming continues the trend of recent anthropogenic warming of 0.07 °C per decade, on average, since 1960[14,18]. Projected warming rates increase slightly with latitudinal zone, from the tropics to polar oceans (Table 1). Remarkably, under RCP8.5, 99% of the world's MPAs are forecasted to warm ≥2 °C by 2100. The RCP4.5 mitigation scenario predicts warming rates roughly 50% lower than those projected for the BAU scenario (Table 1). Under RCP4.5, mean warming rates range from 0.014 °C per year in tropical MPAs to 0.022 in polar MPAs.

The effects of ocean warming on marine species and ecosystems, which are already well-documented[19–22], would likely increase if the rates of warming under RCP8.5 are realized. Several recent studies have combined projected warming, species-specific thermal tolerances and patterns of species distribution to predict

[1]Department of Biology, The University of North Carolina at Chapel Hill, Chapel Hill, NC, USA. [2]Ocean and Earth Science, National Oceanography Centre Southampton, University of Southampton, Southampton, UK. [3]Department of Ocean Sciences, Memorial University of Newfoundland, St John's, NL, Canada. [4]Department of Biological Sciences, Florida Institute of Technology, Melbourne, FL, USA. [5]Marine Conservation Institute, Seattle, WA, USA. [6]Polar Bears International, Bozeman, MT, USA. [7]Department of Zoology and Physiology, University of Wyoming, Laramie, WY, USA. [8]NOAA Atlantic Oceanographic and Meteorological Laboratory, Ocean Chemistry and Ecosystems Division, Miami, FL, USA. [9]Cooperative Institute for Marine and Atmospheric Studies, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL, USA. [10]National Oceanography Centre, Southampton, UK. *e-mail: jbruno@unc.edu

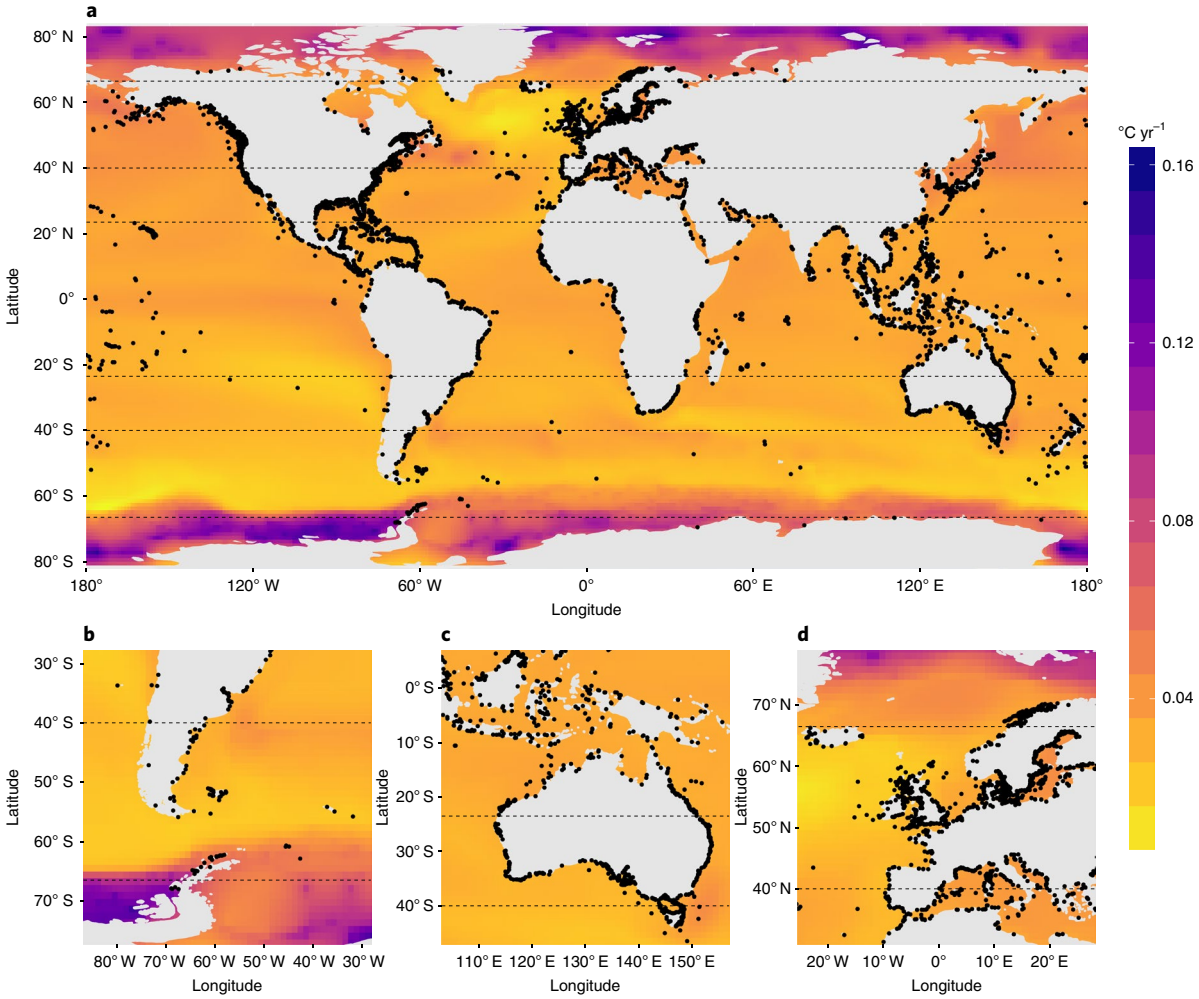

Fig. 1 | Patterns of projected ocean warming. Annual warming rates (colour scale) are based on CMIP5 simulation ensembles under the RCP8.5 emissions scenario, 2006–2100. Black dots are MPAs used in the study.

changes in species richness and composition in response to ocean warming. For example, a previous study[4] predicted that nearly 100% of extant species will be excluded from many tropical reef communities by 2115 under RCP8.5. Likewise, a further study[5] predicted drastic declines in the regional species pools of tropical marine communities and substantial increases in temperate communities, accompanied by changes in species composition. These projected responses are driven by populations tracking the geographic movement of their thermal niches and shifting their ranges, generally to higher latitudes[19,23]. In mid- to high-latitude ecosystems, shifts in species composition will likely lead to changes in species interactions and food-web dynamics, losses of foundation species such as kelps, and invasions of new predators, competitors, and parasites[19,24]. In contrast, as tropical communities cross their thermal thresholds, the primary outcome is expected to be biodiversity loss, as there are no climate-change-induced migrants to colonize from warmer regions. Thus, ocean warming could have fundamentally different impacts on the biota currently protected in tropical and temperate MPAs. Finally, due to temperature-dependent metabolism of fishes and invertebrates, which are ectotherms, warming will have strong, non-lethal effects on a wide array of population-, community- and ecosystem-level processes, including developmental and dispersal rates, species interactions and the standing biomass of plants and animals[21,25–27].

Table 1 | Projected rates of increase of ocean temperature in no-take marine reserves and for MPAs in four latitudinal zones for two different emission scenarios (RCP8.5 and 4.5) based on CMIP5 simulation ensembles (2006–2100).

Metric	Scenario	Reserves (309)	All MPAs (8,236)	Tropical (2,458)	Subropical (2,738)	Temperate (2,874)	Polar (166)
Mean	RCP8.5	0.033 ± 0.004	0.035 ± 0.007	0.031 ± 0.002	0.033 ± 0.003	0.040 ± 0.008	0.051 ± 0.011
Mean	RCP4.5	0.014 ± 0.002	0.015 ± 0.004	0.014 ± 0.001	0.014 ± 0.002	0.018 ± 0.004	0.022 ± 0.002
Max	RCP8.5	0.035 ± 0.006	0.039 ± 0.008	0.032 ± 0.002	0.037 ± 0.004	0.046 ± 0.008	0.058 ± 0.008
Max	RCP4.5	0.015 ± 0.003	0.017 ± 0.004	0.014 ± 0.001	0.016 ± 0.002	0.020 ± 0.004	0.025 ± 0.001

Mean values are the mean annual changes in the mean temperature across units (for example, no-take reserves or all MPAs). Maximum values are the means of the maximum projected values across all units. Errors are standard deviations of estimates of warming rates across MPAs.

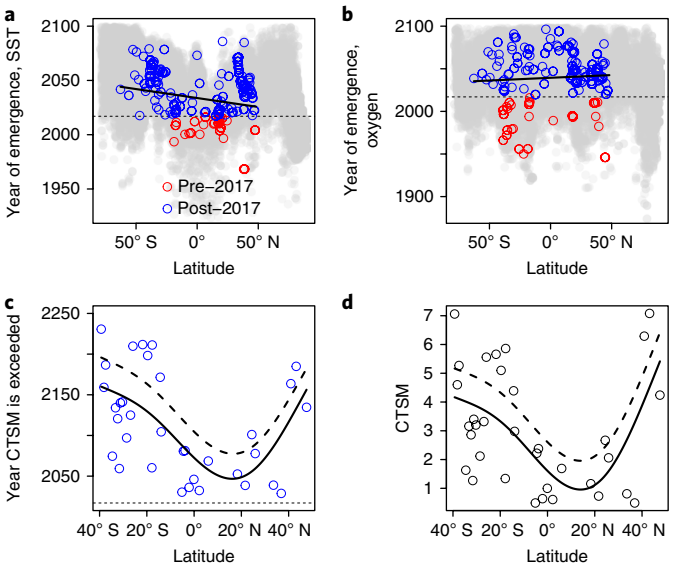

Fig. 2 | Latitudinal patterns of the year that environmental conditions will exceed predicted thresholds. a,**b**, Red circles are fully protected reserves in which thresholds have already been exceeded (in 2017), blue circles are reserves that have not, and grey circles are grid cells not in a marine reserve. Black lines are fitted functions from a generalized additive model that includes a spatial autocorrelation term. **c**, The year that the CTSMs will be exceeded for marine ecoregions (blue circles) based on the predicted mean warming rate (RCP8.5) for all MPAs in each ecoregion (see values in Supplementary Table 1). The CTSM is the average maximum temperature across the geographical ranges (determined with 2,447 in situ surveys by the Reef Life Survey programme[4]) of all species in a community minus the present maximum summertime SST; it is an estimate of how far on average community inhabitants are from their thermal maxima[4]. Note that the latitudinal extents differ in the top and bottom panels due to a lack of data at high latitudes in the RLS data. The geographic pattern for CTSM emergence (**c**) is largely driven by the inherent differences among latitudes in the CTSM[4] (**d**, plotted as °C), which is substantially greater for higher-latitude ecoregions.

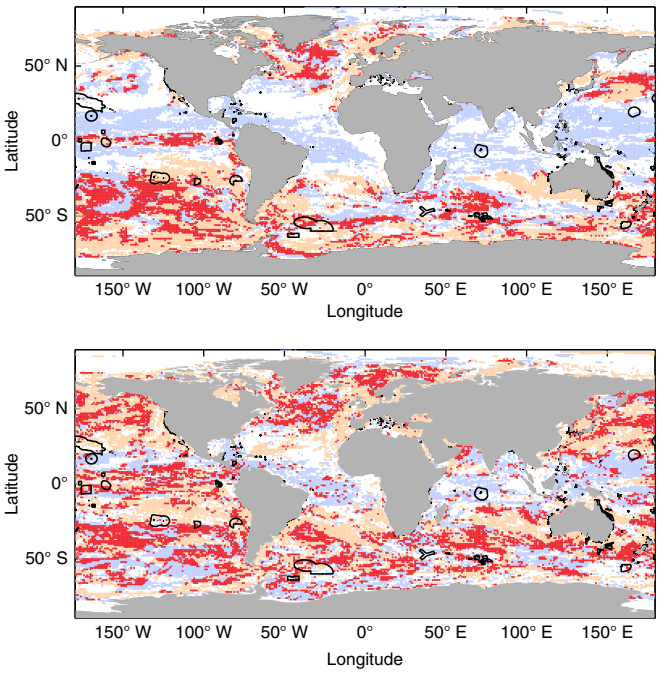

Fig. 3 | Spatial distribution of temporary refugia from climate change and current coverage of MPAs. Areas of the ocean for which SST (orange), oxygen concentration (lilac), and both variables (red) emerge after 2050 for RCP8.5 (business as usual, top panel) and 4.5 (mitigation, bottom panel). MPAs are outlined in black.

Not all of these effects will be realized in every MPA. For example, individuals can acclimatize and populations can adapt to warming. However, there are limits to the scope and rate of both acclimatization and adaptation that vary with phylogenetic history, life history and other biological attributes. Moreover, anthropogenic warming is occurring far more rapidly than natural warming has over the past 65 million years[28]. If emissions quickly peak and stabilize in the next few decades (RCP4.5), forecasted impacts on marine organisms and ecosystems[11,12] would presumably be reduced, although by how much is unclear.

Under RCP8.5, by 2050 trends in warming and deoxygenation, as well as declining pH, all exceed background variability over 86% of the ocean[11]. In fact, pH emerged in all marine reserves decades ago (Supplementary Fig. 1). Assuming organisms are adapted to local environmental conditions, this degree of change in multiple environmental variables that strongly affect their metabolism and fitness, and largely define their fundamental niches, could potentially lead to local extinctions and changes in species composition. We considered this emergence point—the exceedance of natural variability—to be a threshold for population and community responses to climate change[11]. We calculated the year of emergence (that is, the timing of exceedance) of warming and deoxygenation for no-take marine reserves at different latitudes (Fig. 2). Under RCP8.5, both stressors emerge by mid-century in 42% of no-take zones. Unlike deoxygenation (Fig. 2b), the year of emergence for temperature was later by decades for high-latitude reserves (Fig. 2a, but note there is substantial variation at a given latitude). By contrast, temperature has already exceeded background variability for many tropical reserves. For a number of reasons, the effect of exceeding these and other environmental thresholds cannot be predicted with absolute certainty. For one, the realized environmental tolerances and adaptability for most species are unknown. However, given the effects warming in particular is already having on populations of habitat-forming species such as corals[9] and on the geographic ranges of countless taxa[19], further change will likely exacerbate biodiversity shifts away from the tropics and towards higher latitudes.

Warming rates are projected to be relatively modest in some marine ecoregions[29], including many around Australia and New Zealand, and more rapid in others, such as the western Mediterranean and South Orkney Islands (Supplementary Table 1). However, the substantial

Table 2 | Projected rates of increase (mean values of change in °C per year and number of grid cells) of ocean temperatures in MPAs and for entire latitudinal zones (all 1×1° cells) for RCP8.5.

	Tropical	Subropical	Temperate	Polar
MPAs only	0.031 (2,458)	0.033 (2,738)	0.040 (2,874)	0.051 (166)
Zone	0.032 (13,227)	0.031 (9,233)	0.032 (13,940)	0.065 (6,868)

Overall mean rate of the global ocean is 0.0333 °C year^{-1} (N = 43,268 cells). Zone-specific values were based on cell-area-weighted means.

variation in the inherent thermal sensitivity of constituent species (that is, thermal bias[4]) among ecoregions complicates geographic comparison of predicted warming impacts. The margin between what a species can tolerate and local maximum temperatures, averaged across all species in a community, is the 'community thermal safety margin' (CTSM). Exceeding the CTSM means that maximum summertime temperatures exceed the realized maximum for the average species within the community. This could lead to the loss of a substantial number of species, even with a reasonable degree of adaptation or acclimatization[4,5]. Based on predicted warming under RCP8.5, for many tropical ecoregions the CTSM will be exceeded by ~2050 but not until ~2150 at temperate latitudes (Fig. 2c).

One potential management response to anthropogenic warming is to position reserves within regions expected to warm less or not at all, that is, climate change refugia[30,31]. However, forecasted warming rates for MPAs roughly match mean background rates; MPAs are warming at the same rate as unprotected areas, except in polar regions (Table 2). At a smaller scale, we found that there is substantial variation among ecoregions in projected warming (Supplementary Table 1), but that MPA placement has not been focused on ecoregions with lower rates (Supplementary Fig. 2). However, even if future MPAs are better positioned in regard to projected warming, the distribution of other important climate-change stressors such as deoxygenation is spatially discordant with that of temperature (Fig. 3), and may also be decoupled from the inherent sensitivity of communities to these stressors. Locations for which SST emerges after 2050 under RCP8.5 are primarily in the Southern Ocean, whereas refugia from deoxygenation are mainly tropical (Fig. 3). Critically, only 3.5% of existing MPAs overlap with multi-variable refugia (Fig. 3).

Marine biodiversity is already being degraded by numerous stressors unrelated to carbon emissions such as fishing, habitat loss and pollution[32]. Populations of marine vertebrates, especially predators, have been reduced by 50 to 95% in most oceanic regions[33–35], and habitat-forming species such as seagrasses, mangroves and corals are declining by roughly 1% annually[36–38]. Although not a panacea, well-enforced MPAs, particularly no-take marine reserves, effectively mitigate some of these threats and partially restore marine biodiversity[2,39]. A recent meta-analysis found that to meet the biodiversity and fisheries goals of MPAs, global coverage needs to be increased from 4% of the world's oceans to 30% or greater[40]. We support the rapid expansion of fully protected MPAs and other forms of local conservation; however, our findings highlight the critical caveat that local protection is necessary but insufficient to conserve and restore marine biotas[1]. Although MPAs are widely promoted as a means to mitigate the effects of climate change[41], the opposite perspective is more in line with the scientific reality: without drastic reductions in carbon emissions, ocean warming, acidification and oxygen depletion in the twenty-first century will in all likelihood disrupt the composition and functioning of the ecosystems currently protected within the world's MPAs. The community- and ecosystem-level impacts of climate change threaten to negate decades of progress in conservation and further imperil species and ecosystems that are already in jeopardy.

Methods

Methods, including statements of data availability and any associated accession codes and references, are available at https://doi.org/10.1038/s41558-018-0149-2.

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Author contributions

J.F.B., R.B.A. and S.C.A. conceived the study. J.F.B., A.E.B., C.C. and S.A.H. performed the analysis. J.F.B., A.E.B., S.A.H. and R.B.A. interpreted the results. J.F.B., R.B.A. and A.E.B. wrote the manuscript, with substantial assistance from the other authors. A.E.B., E.P.P., R.v.H. and S.A.H. provided datasets.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at https://doi.org/10.1038/s41558-018-0149-2.

Correspondence and requests for materials should be addressed to J.F.B.

Methods

Projected temperature values. SST data were obtained from CMIP5 climate ensembles for both RCP4.5 and RCP8.5 at a spatial resolution of 1 × 1° (archived by the Earth System Grid Federation at: http://pcmdi9.llnl.gov and in this paper's GitHub repository: https://github.com/johnfbruno/MPAs_warming). Cell-specific warming rates for the climate scenarios (RCP4.5 and RCP8.5) were calculated as linear rates of change (°C year^{-1}) for both the annual mean and annual maximum SST, between 2006 (based on observed current temperatures) and predicted 2100 temperatures. These data were saved as raster files and imported into R Studio[42] using the R package raster[43]. We also examined predicted values from a downscaled version (5 km scale) of a model published previously[44]. The downscaling was achieved by adjusting both the annual cycle and mean temperature with observed data from the Pathfinder 5.0 climatology[44]. The 1 × 1° data ranged from 90° N to 90° S whereas the downscaled data ranged from 45° N to 45° S. Because of the geographic restriction of the downscaled data, they were used only to validate the use of 1 × 1° resolution data for the global analysis. This was done by comparing projections between the two datasets within the overlapping geographic extent and testing for bias along a latitudinal gradient (Supplementary Table 2, Supplementary Figs. 3,4). Although projections are very similar, there is minor bias across latitudes between the native and downscaled models: the downscaling procedure produces projections that favour faster warming in the southern hemisphere, whereas the native 1 × 1 models favour faster warming in the northern hemisphere (between 45° N and 45° S).

MPA locations. Coordinates and information for MPAs in the world's oceans were provided by the Marine Conservation Institute[45], based on a database provided by the UNEP-WCMC and IUCN[46]. These coordinates (the centroids of each MPA) are available in this paper's GitHub repository: https://github.com/johnfbruno/MPAs_warming.

Climatic data were extracted from the raster cell closest to the centroid of the spatial polygon for each MPA, and the distance between the raster value and centroid was measured. A downscaled SST raster from Bio-ORACLE[47] was used as a land mask for the CMIP5 ensemble data to filter out unwanted MPA coordinates. To prevent the analysis from including both freshwater MPAs, such as those in the Great Lakes, and MPAs with incorrectly labelled coordinates, extracted cells greater than 50 km away from the MPA centroid were removed from the analysis. The extracted temperature data were then stratified into four groups: (1) polar, ranging from 66.5–90° S and N (n = 166); (2) temperate, ranging from 40–66.5° S and N latitude (n = 2,874); (3) subtropical, ranging from 23.5–40° S and N (n = 2,738); and (4) tropical ranging from 23.5° S to 23.5° N across the equator (n = 2,458). All data and R code used to summarize MPA warming trends (for example, at different latitudes) are archived at GitHub: https://github.com/johnfbruno/MPAs_warming.

Time of emergence calculations. The time of emergence estimates are taken from a previous study[11]; a summary of the approach is given here. Time of emergence is calculated for the annual maxima of SST and the annual minima of thermocline average oxygen concentration. Trends in SST and oxygen are calculated using a generalized least-squares model with a first-order autoregressive error term. The time series of annual extrema in the conjoined historical and warming scenario (RCP8.5) runs is created. An inflection point is then identified by calculating the cumulative sum of the gradient in the time series and finding the year when it exceeds zero (for a negative trend) or drops below zero (for a positive trend) for the remainder of the time series. The trend in the time series is then calculated from the inflection point forward to 2100. The natural variability (that is, noise) is defined using a 100-year section of the model's control run as one standard deviation in the annual extrema time series. The time of emergence (ToE) is then defined as:

$$\mathrm{ToE} = (2 \times \mathrm{noise})/\mathrm{trend}$$

Any values of ToE that exceed 2100 are excluded from the analysis.

Community thermal safety margin analysis. We use the mean thermal bias[48] (TBiasmax) for 34 marine ecoregions, as reported in the Supplementary Table 1. In brief, for each of these ecoregions TBiasmax was calculated as an average across communities sampled within the ecoregion. TBiasmax integrates the average upper temperature occupied across all species in a community with the local temperature to quantify a warming buffer (which we call the community thermal safety margin CTSM). We use this term because the metric is essentially the community-weighted mean for the species' thermal safety margin (TSM): the 95th percentile of species' thermal distributions. It is a measure of realized upper thermal limits across repeated surveys of fish and mobile invertebrates (Reef Life Survey, http://reeflifesurvey.com[49]) minus the mean summer temperatures (quantified for the years 2008–2014) for a particular location in which a species is observed, as described previously[48] (where mean SST is from the eight warmest weeks of each year[50]).

Data availability. Data generated during the study are available in public repositories including within the study's GitHub repository (https://github.com/johnfbruno/MPAs_warming).

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