Climate Change Threatens the World's Marine Protected Areas

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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 (BAU) emissions (RCP8.5)[3] will likely result in further habitat and species losses throughout low-latitude and tropical MPAs[4,5]. With continued BAU emissions, mean sea-surface temperatures (SST) within MPAs are projected to increase 0.034 °C/year and warm an additional 2.8 °C by 2100. Under these conditions, the time of emergence (the year when SST and oxygen concentration exceed natural variability) for 309 no-take marine reserves, is mid-century in 42% of reserves. Moreover, projected warming rates and the existing "Community Thermal Safety Margin" (CTSM, the inherent buffer against warming based on the thermal sensitivity of constituent species) both vary among ecoregions and with latitude. The CTSM 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 BAU 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 already are having substantial effects on populations and ecosystems otherwise protected within terrestrial and marine reserves[7,8]. Gradual warming over the last 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 over 90% of the additional heat being 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, e.g., 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 emissions trajectory RCP 8.5 and the RCP 4.5 mitigation scenario, for which emissions peak around 2040 and CO_2 concentration stabilizes at ~525 ppm in 2100 (ref. 2). We used CMIP5 models to predict the mean 21st century rate of change in SST and O_2 at the geographic centers of 8236 MPAs around the world (Fig. 1A). We also assessed warming and deoxygenation rates in 309 no-take reserves (a subset of the 8236 MPAs), in which fishing is banned.

With BAU emissions, mean SSTs are predicted to increase within nearly all MPAs: the average warming rate is 0.034 °C/year (Table 1), with a maximum increase of 0.113°C/year in northern Baffin Bay off northwest Greenland. This predicted future warming continues the trend of recent anthropogenic warming of 0.07 °C/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 RCP 8.5, 99% of the world's MPAs are forecasted to warm ≥2°C by 2100. The RCP 4.5 mitigation scenario predicts warming rates roughly 50% lower than those projected for the BAU scenario (Table 1). Under RCP 4.5, mean warming rates range from 0.014 °C/year in tropical MPAs to 0.019 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 RCP 8.5 are realized. Several recent studies have combined projected warming, species-specific thermal tolerances, and patterns of species distribution to predict changes in species richness and composition in response to ocean warming. For example, Stuart-Smith et al.[4] predicted that nearly 100% of extant species will be excluded from many tropical reef communities by 2115 under RCP 8.5. Likewise, Molinos et al.[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].

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 last 65 million years[28]. If emissions quickly peak and stabilize in the next few decades (RCP 4.5) forecasted impacts on marine organisms and ecosystems[11,12] would presumably be reduced, although by how much is unclear.

Under RCP 8.5, 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 (Fig. S1). Assuming organisms are adapted to local environmental conditions, this degree of change of 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 (i.e., the timing of exceedance) of warming and deoxygenation for no-take marine reserves at different latitudes (Fig. 2). Under RCP 8.5, 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 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 countess 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 (Table S1). However, the substantial variation in the inherent thermal sensitivity of constituent species (i.e., 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 RCP 8.5, 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, i.e., 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 (Table S1), but that MPA placement has not been focused on ecoregions with lower rates (Fig. S2). 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 RCP 8.5 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]. While we support the rapid expansion of fully-protected MPAs and other forms of local conservation, our findings highlight the critical caveat that local protection is necessary but insufficient to conserve and restore marine biota[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 21st 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.

Supplementary Information is available in the online version of the paper.

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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.

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Methods

Projected temperature values: Sea Surface Temperature (SST) data were obtained from CMIP5 climate ensembles for both RCP 4.5 and RCP 8.5 at a spatial resolution of 1x1° (archived by the Earth System Grid Federation at: http://pcmdi9.llnl.gov and in the papers GitHub repository: https://github.com/johnfbruno/MPAs_warming. Cell-specific warming rates for the climate scenarios (RCP 4.5 and RCP 8.5) were calculated as linear rates of change (°C/year) 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 model (<5km scale) from van Hooidonk et al.[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 1x1° data ranged from 90ºN to 90ºS whereas the downscaled data ranged from 45ºN to 45ºS. Because of the geographic restriction of the downscaled data, it was used only to validate the use of 1x1° 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 (Table S2, Figs. S3 & S4). Although projections are very similar, there is minor bias across latitudes between the native and downscaled models: the downscaling procedure produces projections that favor faster warming in the southern hemisphere, while the native 1x1 models favor faster warming in the northern hemisphere (between 45°N and 45°S).

MPA locations: Coordinates and information for Marine Protected Areas (MPAs) in the world's oceans were provided by the Marine Conservation Institute, based on a database provided by the UNEP-WCMC and IUCN:

> Marine Conservation Institute. (2016). MPAtlas. Seattle, WA. www.mpatlas.org [Accessed Sept 2016] – based on data provided by UNEP-WCMC and IUCN.

> UNEP-WCMC and IUCN (2016), Protected Planet: [The World Database on Protected Areas (WDPA) [On-line], Cambridge, UK: UNEP-WCMC and IUCN. Available at: www.protectedplanet.net.

These coordinates (the centroids of each MPA) are available in the papers 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[45] 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 ones 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° to 90° latitude (n=166); 2) temperate, ranging from 40° to 66.5° latitude (n=2738); 3) subtropical, ranging from 23.5° to 40° latitude (n=2738); and tropical ranging from -23.5° S to 23.5° N across the equator (n=2458). All data and R code used to summarize MPA warming trends (e.g., at different latitudes) is archived at GitHub: https://github.com/johnfbruno/MPAs_warming.

Time of Emergence (ToE) calculations: The ToE estimates are taken from Henson et al. (2017); a summary of the approach is given here. ToE 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 (i.e. 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 is then defined as:

$$ToE = (2\,.\,noise)/trend$$

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

Community Thermal Safety Margin (CTSM) analysis: We use the mean thermal bias[46] (TBiasmax) for 34 marine ecoregions, as reported in the Extended Data Table S1. 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 this metric is essentially the community-weighted mean for the species thermal safety margin (TSM): the 95th percentile of species' thermal distributions - a measure of realized upper thermal limits across repeated surveys of fish and mobile invertebrates (Reef Life Survey, http://reeflifesurvey.com[47]) minus the mean summer temperatures (quantified for the years ranging between 2008 and 2014) for a particular location in which a species is observed, as described in Stuart-Smith et al.[46] (where mean SST from the eight warmest weeks of each year[48]).

Data availability: Data generated during the study are available in public repositories including within the study's GitHub repository.

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Table 1. Projected rates of increase of ocean temperature (mean SST °C / year ± 1 SD = the SD of estimates of warming rates across MPAs) in no-take marine reserves and for MPAs in four latitudinal zones for two different emission scenarios (RCP 8.5 and 4.5) based on CMIP5 simulation ensembles (2006-2100). Mean values are the means annual changes in the mean temperature across units (e.g., no-take reserves or all MPAs). Maximum values are the means of the maximum projected values across all units.

Metric	**Scenario**	**Reserves (309)**	**All MPAs (8236)**	**Tropical (2458)**	**Subropical (2738)**	**Temperate (2738)**	**Polar (166)**
Mean	RCP 8.5	0.033±0.004	0.034± 0.006	0.032±0.002	0.034±0.004	0.036±0.007	0.038±0.013
Mean	RCP 4.5	0.014±0.002	0.015±0.003	0.014±0.001	0.015±0.002	0.016±0.004	0.019±0.009
Max	RCP 8.5	0.035±0.006	0.037±0.007	0.033±0.002	0.037±0.006	0.042±0.007	0.043±0.011
Max	RCP 4.5	0.015±0.003	0.016±0.003	0.014±0.001	0.016±0.003	0.018±0.004	0.021±0.004

Table 2 Projected rates of increase (mean values of change in °C / year and number of grid cells) of ocean temperatures in MPAs and for entire latitudinal zones (all 1x1 degree cells) for RCP 8.5. Overall mean rate of the global ocean is 0.0333 (°C / year, N=43,268 cells). Zone-specific values were based on cell area weighted means.

	Tropical	**Subropical**	**Temperate**	**Polar**
MPAs only	0.032 (2458)	0.034 (2738)	0.036 (2738)	0.038 (166)
Zone	0.032 (13227)	0.031 (9233)	0.032 (13940)	0.065 (6868)

Figure legends

Figure 1. Patterns of projected ocean warming. Annual warming rates (°C/year) are based on CMIP5 simulation ensembles under the RCP 8.5 emissions scenario, 2006-2100. Black dots are MPAs used in the study.

Figure 2. Latitudinal patterns of the year that environmental conditions will exceed predicted thresholds. For 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 GAM that includes a spatial autocorrelation term. c: The year that the Community Thermal Safety Margins (CTSM) will be exceeded for marine ecoregions (blue circles) based on the predicted mean warming rate (RCP 8.5) for all MPAs in each ecoregion (see values in Table S1). The CTSM is the average maximum temperature across the geographical ranges (determined with 2,447 *in situ* surveys by the Reef Life Survey program[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.

Figure 3. Spatial distribution of temporary refugia from climate change and current coverage of Marine Protected Areas. Areas of the ocean for which SST (orange), oxygen concentration (lilac), and both variables (red) emerge after 2050 for RCP 8.5 (top panel) and 4.5 (bottom panel). MPAs are outlined in black.