**Climate change impacts on the global distribution of suitable habitat and protection status of shallow-water coral reefs**

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WHATS LEFT TO DO:

-Include IPSL RCP2.6, 7.0 mpa/reef analysis results

-Include all GFDL mpa/reef analysis results

-Edit abstract

-Select which figures to keep/remove

-Double check references

-Format according to journal

# **Abstract-** edit once full analysis has been done

Anthropogenic climate change is causing impacts on a broad range of marine organisms. At particular risk are calcifying organisms such as Scleractinia (stony corals) which are affected by the twin impacts of warming waters and increasing ocean acidification. As corals are ecosystem engineers that provide habitat for numerous other species, conservation efforts for reef ecosystems, including through spatial conservation tools such as marine protected areas (MPAs), are crucial for helping limit impacts on biodiversity in a changing ocean. Here we use multiple emissions scenarios (high mitigation RCP2.6; intermediate-to-high emissions RCP7.0; high emissions RCP8.5) to project how suitable habitat for shallow-water coral reefs and coverage of this habitat by the global MPA network will be affected by climate change. Under the XXX scenario, we find that by 2100 around 85% of existing reefs were projected to be above a literature-derived thermal threshold of 30ºC, and 97% below a pH threshold of 7.7. The total area of suitable worldwide habitat for reefs declined by 95.4% between the beginning and end of the century. MPA coverage of suitable reef habitat was projected to decline from 735,405 km2 in the present to 64,002 km2 under the assumption of no physiological adaptation, a decline of 91%. However, the proportion of reef habitat within MPAs increased from 50.4% of total reef to 95.1%.While the majority of present-day reefs are found to be in MPAs designated as IUCN categories VI and II (protected areas with sustainable use of natural resources and national parks), while the majority of end of century reefs were found within MPAs designated as habitat/species management areas (category IV) and protected areas with sustainable use of natural resources (category VI). Our analysis helps to inform conservation and management priorities to build resilience for future coral reefs in the face of climate change.

# **Introduction**

Coral reefs, with physical structures primarily formed by stony corals (*Scleractinia*), are one of the most biodiverse ecosystems on our planet (Quek et al. 2020). The Scleractinian order is composed of over 1,500 species that are globally distributed in both warm, shallow waters and cold waters (Quek et al. 2020). Scleractinia are composed of individual polyps that secrete a calcium carbonate skeleton, with shallow water species having endosymbiotic relationships with zooxanthellae, photosynthetic algal symbionts that provide the polyps with nutrients and waste removal (Lough et al. 2018). Both shallow- and deep-water Scleractinia, and in particular reef-forming species, are important ecosystem engineers that provide other species with shelter and food (Lough et al. 2018). In addition to housing complex and diverse ecosystems, coral reefs can also play an important socio-economic role for coastal communities through provision of ecosystem services and benefits such as fisheries, recreation, tourism and biogeochemical cycling (Hughes et al. 2017). The diversity of species that coral reefs attract are an important source of food and income, and the structure of reefs can offer protection to nearby coastal communities (Hughes et al. 2017), while their natural beauty holds a significant cultural/intrinsic value (Larson et al. 2015).

These important ecosystems, however, are threatened by anthropogenic climate change, through both ocean acidification and warming waters. The ocean stores large amounts of atmospheric carbon dioxide (CO2) and has increasingly been doing so since the industrial revolution (Orr et al. 2005). When CO2 becomes dissolved in seawater, it reacts to release bicarbonate, lowering the pH and reducing the availability of the carbonate ions that calcifying organisms such as tropical shallow-water stony corals use to create their skeletons, and altering the balance between accretion and dissolution (Cotovicz et al. 2020; Eyre et al. 2018; Watson et al. 2017). Moreover, the increase in atmospheric greenhouse gases has resulted in associated increases in sea surface temperatures (SST) (Hughes et al. 2017). When subjected to elevated water temperatures for an extended period, shallow-water coral polyps expel the endosymbiotic zooxanthellae that live within them and lose their coloration, a phenomenon commonly referred to as “bleaching” (Hoegh-Guldberg et al. 2007). Following a bleaching event, corals may suffer from reduced growth and calcification, with survival rates declining (Ostrander et al. 2000).

In addition to the ongoing and accelerating impacts of climate change, the continued exposure of coral reefs to other anthropogenic stressors such as overfishing and pollution further increases their vulnerability as the cumulative or synergistic effects of multiple stressors may overwhelm the ecosystem (Renfro and Chadwick 2017. The multi-causality of this suite of impacts can drastically alter species composition, habitat structure, associated biodiversity, and key ecosystem functions. In the face of these multiple stressors, a range of management and conservation tools are used to help protect reefs and their associated biodiversity, including spatial management tools such as marine protected areas (MPAs). By limiting the level and types of human impacts on ecosystems such as coral reefs, MPAs may help build resilience to climate impacts. Yet the extent to which the efficiency and effectiveness of MPAs may be challenged by climate change, and how the changing distributions of species will affect coverage by MPAs, remain open questions (Tittensor et al. 2019).

Here, we explore the future of coral reefs and their management and conservation through MPAs by first projecting the effects of increasing SST and ocean acidity on the global area of suitable habitat for tropical, shallow-water reefs over the coming century. We then compare the global distribution of coral reefs covered by the present day MPA network with the proportion that both remain in suitable habitat and are covered by the same MPA network in 2090-2100, and further evaluate this coverage based on the management practices within these MPAs. While additional areas of suitable habitat for corals may appear, the slow growth rate and production of reefs (REF, REF) mean that protecting existing coral reef habitat remains of crucial importance. Similarly, while new MPAs can be designated to help protect additional areas of the ocean, evaluating the coverage of the existing network for coral reefs that are likely to remain at the end of the century helps to identify gaps and provide a baseline on how changes in reef suitability will impact this network.

**Materials and Methods**

We combined data on present-day coral reef distributions with present-day and projected sea-surface temperature (SST) and pH values to analyzed the proportion of reefs that are remain in suitable habitat in 2100, using a literature review to assess niche thresholds to determine whether habitat remained suitable under climate change. These present-day distributions and remaining suitable future habitat were then compared to the global MPA network, including the IUCN protected area categories for each MPA, to determine the proportion of reefs that are expected to both remain in suitable habitat and within marine protected areas of different types. Details of our methodology are provided below.

## *Coral reef distribution:*

Data on the global distribution of coral reefs was downloaded from the United Nations Environment Programme World Conservation Monitoring Centre website (UNEP-WCMC et al. Version 4.1 2021). This dataset compiles the location of warm-water coral reefs worldwide from a number of sources (Andréfouët et al. 2006), representing a variety of reefs, shoals, banks, and patches, with data gathered from 1954-2009. In total there were 17,504 reefs included in a spatially explicit form (polygons), and 925 included as points only. We excluded point locations from our study, since they did not specify the area nor extent of the coral reefs found therein.

## *MPA distribution*

The global distribution of MPAs was downloaded from the Protected Planet website (UNEP-WCMC and IUCN 2021). Each MPA was classified according to the IUCN’s Protected Area Categories (Dudley et al. 2013). In total, there were 17,300 MPAs included as polygons, of which 104 were designated as other effective area-based conservation measures (OECMs), and 1,610 additional MPAs which were represented only as points. As points did not specify the area or extent of the MPA, they were excluded from further analysis. We included all MPAs from the database in our analysis including those that are proposed, inscribed, adopted, designated or established (UNEP-WCMC 2019). also

Table 1 Classifications and brief descriptions for the six listed categories of the IUCN Protected Area Categories System according to Dudley et al. (2013), and inferred protection for coral reefs.

|  |  |  |  |
| --- | --- | --- | --- |
| IUCN Protected Area Categories System | | | |
| **Category:** | **Classification:** | **Description:** | **Inferred protection for coral reefs:** |
| Ia. | Strict Nature Reserves | Areas considered high risk for either species, ecosystems or geographic features.  Involve little to no human intervention  They maintain natural values, protect some the Earth’s rarest richness and provide ideal locations for assessing the effects of human impacts. | Reefs would suffer very little from non-climate anthropogenic disturbance and would be highly protected. |
| Ib. | Wilderness Area | Aim to preserve and protect natural areas that have been relatively undisturbed by human activity, while allowing indigenous communities to maintain customs and benefit from non-material natural resources. | Coral reefs located within these areas would have some impacts anthropogenic sources, but practices would be of low intensity, thus posing little threat. |
| II. | National Park | National parks are vast, largely natural areas, that aim to protect ecological processes while promoting educational, recreational and cultural connections between humans and nature. | Reefs may attract more human activity, and potentially be impacted but this may be through sustainable, economic activities, such as ecotourism. |
| III. | Natural Monument or Feature | A natural monument or feature is designated to protecting a specific small area that generally brings in a high value. | Reefs may attract more human activity, but will typically do so through sustainable, economic activities, such as ecotourism for example. |
| IV. | Habitat/Species Management Area | Areas that are actively monitored and adapted in order to effectively protect key areas or species. | Reefs located within these areas may have differing levels of protection for specific species or habitats, depending on the management regime, and use intensities may be higher. |
| V. | Protected Landscape/Seascape | Protected landscape/seascapes have a goal of protecting areas that maintain biodiversity conservation while promoting a sustainable use or enjoyment of the natural environment. | Reefs located within protected seascapes may suffer from high levels of human use, especially through extensive recreational and cultural use. |
| VI. | Protected Area with sustainable use of natural resources | Aims at protecting large scale natural ecosystems that can be used at a low-scale industrial level. They promote the sustainable use of natural resources for economic benefits to local communities. | Reefs located in these areas may have higher levels of human use, and hence likely the highest level of anthropogenic disturbance of all seven categories.  NEED TO DISCUSS ALL OF THESE FURTHER |

*Determining SST and pH thresholds for reefs*

HERE YOU NEED TO LAY OUT THE RATIONALE FOR USING SST AND pH, AND EXPLAIN HOW VALUES WERE EXTRACTED FROM THE LITERATURE. AT PRESENT IT IS UNCLEAR HOW SST AND PH VALUES ARE ACTUALLY USED IN RELATION TO REEFS.

Coral species can display a variety of upper thermal bleaching thresholds when exposed to thermal stress. However, it is estimated that most low-latitude tropical reefs cannot persist beyond a threshold of 30°C (Wooldridge 2009). In fact, a study conducted by de Oliveira Soares et al. (2019) on Scleractinian corals in the equatorial waters of Brazil found that approximately 90.9% of corals experienced strong bleaching in waters that ranged between 26.7º-29.6ºC, suggesting that 30°C represents a fairly conservative upper thermal threshold. Moreover, most corals in this area already experience higher than average annual SSTs of >26ºC, with a variability of 2ºC, and therefore largely represent the upper end of thermal stress that can be endured by Scleractinian coral (de Oliveira Soares et al. 2019). Similarly, Fabricius et al. (2011) found that the ecological composition of tropical coral reefs is severely compromised as surface ocean pH approaches values below 7.7, corresponding to atmospheric CO2 emissions exceeding 750ppm. In addition, Camp et al., (2016) found that coral species subjected to pH levels of 7.8 experienced decreased photosynthesis and calcification rates, regardless of whether they were found in habitats that experience high or low pH variance. Although some corals have the potential to withstand higher SST or lower pH values, the effects of increasing thermal stress and ocean acidity pose a threat to the healthy survival of reefs. Given the findings above, we assume that tropical, shallow-water reefs and aggregates will be severely comprised and habitat become unsuitable for their persistence when subjected to SST and pH values beyond 30ºC and below 7.7 respectively (Wooldridge 2009; Fabricius et al. 2011). These represent conservative values because… [TRY TO FIND MORE PAPERS SHOWING BAD THINGS HAPPEN BEFORE YOU HIT THESE THRESHOLDS].

*Climate change scenarios*

Projections of the effects of climate change on oceanographic conditions can be made through earth-system models (ESMs) informed by the greenhouse gas (GHG) concentration scenarios known as Representative Concentration Pathways, or RCPs (van Vuuren et al. 2011; Lund et al. 2019). While RCP2.6 represents the lower end of GHG concentrations for the coming century, and we refer to it henceforth as ‘high mitigation’, RCP8.5 follows an assumption of high GHG emissions until the end of the century, and we refer to it as ‘high emissions’ (Bryndum-Buchholz et al. 2019). The more recent RCP7.0 scenario represents the outcome expected to occur under weak pollution control as well as high climate mitigation and adaptation (Lund et al. 2019). Under RCP2.6 it is estimated that mean SST will increase by 1.1°C by 2XXX relative to XXXX, while ocean surface pH will decrease by 0.15 units (Magnan et al. 2016). However, under RCP8.5, SST is estimated to increase on average by 3.2°C while ocean surface pH is projected to decrease by 0.41 units (Magnan et al. 2016).

## *SST and surface ocean pH*

Sea surface temperature (Figs 1,2) and ocean acidity (Figs 3,4) were downloaded via the ISI-MIP project (Frieler et al. 2014), which provides standardized grids of oceanographic data derived from Earth System Models (ESMs) from the sixth phase of the Coupled Model Intercomparison Project (CMIP6) (Eyring et al. 2016). Here we used outputs from the IPSL-CM6A-LR (Boucher et al. 2020) and GFDL-ESM4 (Tittensor et al. 2021) models, and projections from RCP2.6, 7.0 and 8.5 scenarios (Bryndum-Buchholz et al. 2019; Lund et al. 2019). ESM outputs, and the temporal resolution was monthly for SST and annual for surface ocean pH (Taylor et al. 2020).We used mean values from 2000-2010 as a reference decade, while projections for 2090-2100 were used to evaluate climate-driven changes over this century.

Results provided follow the IPSL-CM6A-LR ESM (Boucher et al. 2020), whereas the GFDL-ESM4 ESM was used simply as a test of robustness for the purpose of study, demonstrating similar results across two different ESM. Two earth system models and three climate-change scenarios were chosen in order to evaluate projections over a range of plausible outcomes. Moreover, RCP2.6, 7.0 and 8.5 were chosen as they represent the results that can be expected to occur under strict mitigation efforts, average mitigation efforts and a "business-as-usual” situation respectively (Riahi et al. 2017; Bopp et al. 2013).

A map of the world

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Figure 1 Mean SST (in ºC) from 2000-2010. Data from the IPSL-CM6A-LR earth-system model as regridded by ISI-MIP (Kwiatkowski et al. 2020; Frieler et al. 2017).

A map of the world

Description automatically generated with medium confidence

Figure 2 Projected mean SST (in ºC) for 2090-2100. Data from the IPSL-CM6A-LR earth-system model and projected under the RCP8.5 scenario as regridded by ISI-MIP (Kwiatkowski et al. 2020; Frieler et al. 2017).

Graphical user interface, map

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A map of the world

Description automatically generated with medium confidenceFigure 4. Projected mean surface ocean pH levels for 2090-2100. Data from the IPSL-CM6A-LR earth-system model and projected under the RCP8.5 scenario as regridded by ISI-MIP (Kwiatkowski et al. 2020; Frieler et al. 2017).



## *Analysis*

locationlocations to evaluate tpresent-day within, and this was broken down further by IUCN category. This was then repeated but with the current reef distribution modified to remove areas that were above the SST threshold or below the pH threshold under the 2090-2100 ESM projections, with the assumption that reefs will no longer be able to persist in these areas as the environmental conditions will become unsuitable. This then provided an estimate of the total area in which reefs are likely to persist to the end of the century, the total area likely to remain covered by the existing MPA network, and the change in proportion covered by MPAs under each IUCN category. We also evaluated the robustness of the selected SST and pH threshold for coral reef persistence by spatially comparing 2000-2010 SST and surface ocean pH values from the ESMs above against the current distribution of coral reefs..

We repeated the steps outlined above once more for all RCP scenarios under both ESMs. Reef proportions were distributed according to an SST range of 20-35ºC and a surface ocean pH range of 7.6-8.2 to include the proportion of reefs that can be found above and below the established SST and pH thresholds for the entire century.

Data analysis and manipulation were conducted in R version XXXX using the raster (Hijmans 2020, v. 3.4-5) and sf (Pebesma 2018) packages.

# **Results**

## 

## *Present-day coral reefs Reefs and present/future SST and pH conditions under IPSL-CM6A-LR*

Most reefs were located in areas where the mean annual SST in 2000-2010 was between ~20-31°C (Fig 5). Approximately 41% of all shallow-water reefs were found in areas with mean SST values of between 29-30°C in 2000-2010 (Fig 5), with only 1.5% of reefs in 2000-2010 found in waters with mean SST values exceeding the thermal threshold identified for this study, with the maximum observed mean SST value being 32ºC (Fig 5). In contrast, projections of 2090-2100 SST, under RCP8.5 suggested that most reefs would primarily be located within a mean SST range of ~27-35°C in 2090-2100, with approximately 85% of total reefs found in unsuitable habitat with temperatures exceeding the thermal threshold of 30°C (Fig 6). Under RCP7.0, approximately 77% of total reefs were projected to be found above 30ºC in 2090-2100, while only 33% of total reefs were above the thermal threshold in 2090-2100 under RCP2.6.

Chart, histogram

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Figure 5 Proportional distribution of reefs according to mean SST levels in 2000-2010 (UNEP-WCMC et al. 2021). Dashed line represented the identified maximal thermal threshold of 30ºC.

Chart, histogram

Description automatically generated

Figure 6 Proportional distribution of reefs according to mean projected SST levels in 2090-2100, under RCP8.5 (UNEP-WCMC et al. 2021; Kwiatkowski et al. 2020, Frieler et al. 2017). Dashed line represented the identified maximal thermal threshold of 30ºC. Please note that y-axis is set from 0-0.5.

In the contemporary ocean, the vast majority of reefs were found in areas with mean 2000-2010 surface ocean pH values between approximately 8.0-8.1, no reefs found below the pH threshold of 7.7 (Fig 7). Over 30% of all reefs had a surface ocean pH value between 8.04-8.05 in 2000-2010 (Fig 7). Under RCP8.5, projections suggested that the majority of reefs would be found within a mean surface ocean pH range of approximately 7.6-7.8 by the end of the century, with 97% of reefs projected to be found below the threshold of 7.7 (Fig 8). However, no reefs were projected to be in waters below the threshold of 7.7 by the end of the century under both RCP7.0 and 2.6.

Chart, histogram

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Figure 7 Percentage distribution of reefs according to mean surface ocean pH levels in 2000-2010 (UNEP-WCMC et al. 2021). pH is represented by the logarithmic pH scale and the dashed line represents the maximal ocean acidity threshold of 7.7.

Chart, histogram

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Figure 8 Percentage distribution of reefs according to the projected mean surface ocean pH levels in 2090-2100, under RCP8.5 (UNEP-WCMC et al. 2021; Kwiatkowski et al. 2020, Frieler et al. 2017). pH is represented by the logarithmic pH scale and the dashed line represents the maximal ocean acidity threshold of 7.7.

The total area of present-day reefs was around 1.46 million square kilometres (Fig 5). By the end of the century, of this area, the fraction projected to remain within suitable thermal and pH conditions was around 67,300 km2, a decline of ~95.4% under RCP8.5 (Fig 9). The results under RCP2.6 and RCP7.0 are…

Map

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Figure 9 Map of the projected global distribution of coral reefs, shown in green, in 2090-2100 (UNEP-WCMC et al. 2021).

*Coral reefs within MPAs under IPSL-CM6A-LR*

Chart, bar chart

Description automatically generatedOf the total area (1.460 million km2) of present-day coral reefs, approximately 735,000 km2 (~50.4%) are found with the global MPA network (>14.X million km2). Most were in category VI – protected areas with sustainable use of natural resources (Fig 10). Category VI represented a total area of 289,621.5km2 of reefs (39% of total reef area within MPAs) of reefs, while national parks (II) represented a total area of 247,154.9km2. Habitat/species management areas (IV), strict nature reserves (Ia), protected seascape/landscapes (V), wilderness areas (Ib) and natural monument/features (III) represented a total area of 94,431.82km2, 61,463.2km2, 29,020.69km2, 10,758.57km2 and 2,954.641km2 of reefs respectively (Fig 10).

Figure 10 Total area of present-day reefs (in km2) contained within MPAs, classified according to the IUCN Protected Area Categories, in 2000-2010 (UNEP-WCMC et al. 2021; UNEP-WCMC and IUCN 2021).

In contrast, based on the existing global network of MPAs and the projected remaining fraction of present-day coral reef area that remains suitable for reef persistence, ~64,002km2 of reefs were found within MPAs in 2090-2100 (~95.1% of the remaining (~67,300 km2 suitable reef habitat area) (Fig 11). This represents a substantial increase in the proportion protected (XX%), but a large decline in the total area protected (XX km2; YY%). The majority of protected reefs (20,751.66km2 ) in 2090-2100 were found in MPAs classified as habitat/species management areas (IV) (32% of total MPA coverage of reefs in 2090-2100) (Fig 11). This represents a decrease of roughly 74,000 km2, or a 20% proportional decrease, between the beginning and end of the century. Furthermore, protected areas with sustainable use of natural resources (VI) covered a total area of 11,979.69km2 of reefs in 2090-2100, a decrease of roughly 277,642 km2 (95.9%) between the beginning and end of the century (Fig 11). National parks (II) and strict nature reserves (Ia) had a coverage of 10,364km2 and 8,708.412km2 of reefs respectively in 2090-2100 (Fig 11). Wilderness areas (Ib) and protected seascapes/landscapes (V) covered roughly the same total area of reefs with values of 5,842.701km2 and 5,864.053km2 by the end of the century (Fig 11). Finally, only 491.5562km2 of reefs projected to remain in suitable habitat in 2090-2100 were found in MPAs classified as natural monument/features (III) (Fig 11).

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Figure 11 Total area of reefs (in km2) contained within MPAs, classified according to the IUCN Protected Area Categories, in 2090-2100 (UNEP-WCMC et al. 2021; UNEP-WCMC and IUCN 2021).

*Analysis under GFDL*

Under the GFDL-ESM4 ESM, approximately only 1.2% of present-day reefs wer found in conditions where SST is below 30ºC, representing a 0.3% difference between IPSL-CM6A-LR. Under RCP scenarios 8.5, 7.0 and 2.6, approximately 73%, 68% and 29% of reefs are expected to be found in areas where the SST exceeds the thermal threshold of 30ºC, representing a 12%, 9% and 3% difference respectively between the two earth system models. No present-day reefs were found in areas where pH was below the threshold of 7.7, representing a difference of 0.01 pH units between the two ESMs. Under RCP8.5, only 39% are expected to be found below 7.7 under GFDL with the lowest pH expected to be 7.65. This, in contrast to IPSL-CM6A-LR, represents a 58% difference, although the lowest pH is expected to be 7.67, representing a 0.02 pH units difference. Results under RCP7.0 and 2.6 are similar between the two earth system models, with no reefs expected to be below 7.7 in either scenario, and 0.02 and 0.01 differences in pH units respectively for the expected highest pH values.

# **Discussion**

Our findings suggest that by the end of the century, a large proportion of present-day reefs will be located in areas that exceed conservative thresholds for either SST or pH tolerances, or both. Under the assumption that reefs will no longer persist in these regions, this represents a total areal decline of 95.4%. The total area of reefs covered by MPAs decreased from 735,405km2 in 2000-2010 to 64,002km2 in 2090-2100, a decline of 91%. However, the proportion of reefs covered by MPAs increased from 50.4% in 2000-2010 to 95.1% in 2090-2100. These values suggest that there will be a greater decline in reefs remaining in suitable habitat outside of MPAs than inside, emphasizing their importance in reef conservation. Of the area that remains in suitable environmental conditions within MPAs, this shifted from being predominantly IUCN categories VI and II in 2000-2010, to IUCN categories IV and VI in 2090-2100.

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## *Coral reefs and present day/future SST and pH conditions under IPSL-CM6A-LR*

At the beginning of the century, 98.5% of all reefs were found to be in areas where mean SST was below the identified maximal thermal threshold of 30°C (Fig 5). However, 40% of reefs were within only 1°C of the thermal limit (Fig 5). These findings match previous studies which have demonstrated that many corals, and their associated algal symbionts, are currently found living close to their thermal maximums (Middlebrook et al. 2008) and also provide support for the selected thermal threshold (Wooldridge 2009), with very few reefs found beyond this. Furthermore, given that the reef data were collected over a large time-span from the 1950s onwards, and that the oceans have warmed since then, it is possible that the small fraction of reefs beyond this threshold were observed and recorded when the waters were cooler. With sea surface temperatures projected to increase over the coming century, the area of reefs subjected to thermal stress will also increase (Middlebrook et al. 2008). Such statements are corroborated by our results which indicated that in 2090-2100, under RCP8.5, more than 85% of total current reef area would be found above the thermal threshold of 30°C, therefore classifying them as reefs of concern for the analysis (Fig 6). In fact, approximately one-third of reefs were projected to be found 2-3°C above the thermal threshold (Fig 6), and are likely to suffer from severe coral bleaching due to exposure to elevated sea surface temperatures (Middlebrook et al. 2008). This remains conservative because we only considered mean annual temperature and not extreme events and fluctuations; maximum temperatures and heat-waves are likely to cause additional stress (Roth et al. 2021).

Nonetheless, there remains the possibility of some reefs to perish well below the thermal threshold of 30ºC. For instance, Woolsey et al., (2015) found that the thermal tolerances of five Scleractinian species in their early life stages varied between environments found at the same latitude, with the maximal threshold being 30ºC at one end, and 26ºC at the other. Similarly, between 2000-2010, all coral reefs were found to be above the surface ocean pH threshold value of 7.7, with only 3% of reefs associated with a pH value below 8.0 (Fig 7). As atmospheric CO2 concentrations during this time period were of approximately 380ppm (Feely et al. 2004), most pH values in the ocean would have been between 8-8.4 during this time (Soriano-Santiago et al. 2013). Most (79%) of reefs were in waters with pH values of 8.035-8.065 from 2000-2010 (Fig 7). Under the RCP 8.5 scenario it is projected that, by the end of the century, average atmospheric CO2 concentrations will reach values near 800ppm, corresponding to a pH drop of 0.4 units in many surface waters (Feely et al. 2004). Based on IPSL? earth-system model projections, almost 97% of reef area will shift to average surface ocean pH values of 7.7 or lower (Fig 8). Consequently, almost all reefs will fall below the pH threshold of 7.7 by 2090-2100, exposing them to decreased rates of calcification (Fabricius et al. 2011). Calcification rates in hard corals have been shown to be reduced by 55-75% when exposed to waters with pH values below 7.7 (Fabricius et al. 2011). Moreover, reefs found in areas of elevated surface ocean pH lost structural complexity by a factor of three-fold (Fabricius et al. 2011). In total, therefore, under the RCP8.5 (high emissions) scenario, 85%, 97% and 97% of reefs were projected to be found in areas that are beyond thermal thresholds, pH thresholds, or both by 2090-2100. This means that these reefs are likely to suffer from substantial stress (Middlebrook et al. 2008; Fabricius et al. 2011), with the consequence that the total global area of reefs is likely to dramatically decline.

NEED TO DISCUSS OTHER RCP RESULTS MORE IN THIS SECTION.

*Reefs within MPA under IPSL-CM6A-LR*

Under the assumption that coral reefs will not persist in areas beyond environmental thresholds, the total global area covered by reefs declined from 1,460,313.3km2 to 67,287.3km2 between the beginning and end of the century under RCP8.5, representing a decline of 95.4%. In addition, there was a drastic projected decrease in the area of coral reefs within the existing global MPA network, from ~735,000 to ~64,000km2 (a decline of 91%). Yet the proportion of reef area area of reefs found outside MPAs decreased from 49.6% to4.88% of total reef area), meaning that, while the total area of existing protected reefs will likely decline dramatically, of those that remain, over 95% reefs will be contained within existing MPAs by the end of the century, assuming that these MPAs remain in place. The establishment of MPAs around coral reefs is increasingly viewed as one of the more effective management practices needed to protect threatened reefs (Abelson et al. 2016). By directly buffering reefs from other regional stressors such as overfishing, destructive tourism and nutrient loading, MPAs allow reefs to focus on building resilience to the global effects of climate change, which include increasing SST and surface ocean pH (Selig et al. 2012). However, it is critical that anticipated climate change impacts, including effects on suitable habitat for different species, be incorporated into MPA design and operation (Harvey et al. 2018; Tittensor et al. 2019).

Breaking the results down by IUCN category (Fig 10), the largest area of reefs within MPAs were found in MPAs classified as protected areas with sustainable use of natural resources (VI) and national parks (II) at the beginning of the century. By proportion within each MPA category, projections for the end of the century suggest similar results since, once again, the majority of reefs were found in both strictly protected areas (category IV specifically) and sustainable use areas (category VI specifically) (Fig 11) (Crouzeilles et al. 2013). However, the total area of reefs found within each category was reduced, often dramatically so. Roughly 39% of reefs contained within MPAs in 2000-2010 were represented by category VI, yet by the end of the century they only represented around 18% of total reef area (Fig 10, Fig 11). According to Dudley et al., (2013) MPAs designated as category VI are projected to, in the face of climate change, shift from areas with sustainable management practices to areas that are largely unsuitable for reef growth, and some have argued that category VI protected areas […] (Shafer 2020). Therefore, it is possible that the degree of environmental degradation or species extraction occurring within this category may extend beyond the ecological threshold of ecosystems (Shafer 2020), thus futher affecting the reefs found within category VI even at the end of the century.

Ccategory II and IV MPAs represented roughly 33% and 13% of reef area in 2000-2010 and 16% and 32% in 2090-2100 respectively (Fig 10, Fig 11). CAN YOU SAY SOMETHING ABOUT THESE LIKE YOU DID FOR CAT VI ABOVE?

Category IV MPAs can play a key role in biodiversity conservation but can fail to do so when climate change leads to a loss of the conditions required to do so (Dudley et al. 2013). In contrast, reefs found within MPAs classified as national parks (II) would be more resilient to the effects of climate change since much of the natural habitat is unmodified (Dudley et al. 2013). The major threat climate change would pose to category II reefs is a loss of income through tourism, which would affect nearby coastal communities (Dudley et al. 2013). Despite this socio-economic impact on category II reefs, it is likely that MPAs of categories III or lower (categories III, II, Ia, and Ib) offer reefs the best chance at survival under climate change due to the stricter management practices employed and more restrictive uses permitted in these areas. Without the addition of new MPAs to the global network, our results suggest that only ~40% of global reefs within MPAs that remain in suitable environmental conditions will be found in MPAs (categories Ia- III) by the end of the century (Fig 11). ADD IN SOMETHIBG ABOUT NEOLI SOMEWHERE IN THIS PARAGRAPH – EDGAR ET AL 2014 NATURE, I.E. EVEN CATEGORY 1-3 MPAS MAY NOT BE EFFECTIVE IF THEY ARE NOT WELL ENFORCED ETC.

*Growth of the global MPA network and new areas of suitable habitat for coral reefs*

The global MPA network is expanding, and ambitious targets such as 30x30 (REF) suggest that this process will continue. Our analysis only evaluated coral reefs against the existing MPA network, as it is not possible to anticipate future additions or changes to this network. Nonetheless, our study sheds light on how this network in its current configuration can help protect those reefs that remain within suitable environmental conditions for persistence under climate change – and highlights the challenge that many reefs within existing MPAs will no longer be in suitable environmental conditions over the coming century. This emphasizes, that , while they can help build resilience, MPAs alone will not suffice in effectively preserving coral reefs and other habitats from the impacts of climate change worldwide (Tittensor et al. 2019). [ADD IN SOMETHING ABOUT CLIMATE CHANGE MITIGATION USING THE RCP2.6 RESULTS HERE]. While adding new sites to the global MPA network will clearly provide biodiversity conservation benefits, and our analysis identifies gaps in this network for future reef protection, mitigation will clearly play a crucial role in long-term outcomes.

In addition to the global protected area network expanding, it is entirely likely that new areas of the global ocean will become suitable habitat for coral reefs, since some areas that are at present too cool for coral reefs will likely warm sufficiently to make them suitable. Here, we only looked at impacts on existing coral habitat, not potential expansions However, given the timescales for reef establishment (REF, REF), any growth in coral reef area to offset losses will likely not occur by the end of the century. Furthermore, while new parts of the ocean may become suitable in terms of thermal conditions, pH levels are dropping over most of the global ocean (Fig. XX), and light levels and seasonality are much more variable in the higher latitude areas of the global ocean which may become suitable in terms of their mean temperature. These factors may also limit potential expansion.

## *Assumptions & caveats*

Our analysis assumes that the identified thermal threshold remains a barrier, and does not incorporate any potential impacts of adaptation to new environmental conditions. Coral species have been demonstrated to adapt to changing sea surface temperature levels through processes of natural selection of temperature resistant coral polyps or algal symbionts, as well physiological acclimation (Safaie et al. 2018). Moreover, different coral species can also possess different thermal tolerances (McClanahan et al. 2020). For instance, reefs found within the Indo-Pacific Coral Triangle are distributed at higher temperatures than those found outside the Coral Triangle (McClanahan et al. 2020). Similar findings have been made for the tolerance of different coral species various pH levels (Barkley et al. 2017). Coral reefs located in the community of Palau’s karstic Rock Island are currently living at, and continue to persist at, pH levels expected to be reached by the end of the century, i.e. values around 7.7 (Barkley et al. 2017). Similarly to reefs adapted to elevated SST levels, it is presumed that pH tolerant corals arise through processes of adaptation by natural selection or by a precise combination of environmental conditions (Barkley et al. 2017). For instance, McCulloch et al., (2012) demonstrated that some species of Scleractinian coral, such as *Cladocora caespitosa,* possess the ability to up-regulate pH, allowing them to continue calcareous growth despite increasing ocean acidification.

For the purposes of our research, it was assumed that there would be no phenotypic nor genetic adaptation by coral species, nor aggregates, to changing SST and surface ocean pH over the coming century. Furthermore, we assumed that, regardless of their pre-disposition to higher SST and lower pH tolerances, all hard coral species would be impacted similarly by the climatic effects expected to occur when SST and pH levels surpass 30ºC and go below 7.7 respectively, although the evaluation of present-day reef distributions against the SST threshold in particular appear to support this. These assumptions allowed for the analysis of global reefs under both ESM models and RCP scenarios 2.6, 7.0 and 8.5, regardless of a predisposition to adaptation/ acclimation or elevated thresholds. However, this in turn means that there is the possibility for a proportion of reefs found in challenging conditions within our results to continue to persist despite being beyond the identified thresholds.

Finally, thresholds for SST and surface ocean pH tolerance are derived from published studies in the literature, and it is assumed that results found in literature apply directly to our research, despite differing spatial and temporal resolutions and local variation. Nonetheless, even given the assumptions and caveats above, the fact that we are using mean SST values rather than maxima, suggests that these are reasonable first-order assumptions to make.

## *Data limitations*

As previously indicated, both the point data for the current global distribution of MPAs (UNEP-WCMC and IUCN 2021) and reefs (UNEP-WCMC et al. 2021) were excluded from the analysis as they did not specify area nor extent. However, this represented a relatively small fraction of reefs (5.01%) and MPAs (8.62%), and without the area data it was impossible to include these in the analysis. Additionally, over 8485.33x103 km2 of MPA area, or approximately 36% of total MPA area, was classified as not assigned, not applicable or not reported for the IUCN Protected Area category by the data provider (UNEP-WCMC 2019). Therefore, more reefs than those used for our analysis are contained within MPAs, but as they lacked an IUCN category classification, it was not possible to evaluate them in this context.

Results regarding the total reef area were calculated using data from the United Nations Environment Programme World Conservation Monitoring Centre website (UNEP-WCMC et al. Version 4.1 2021). However, differing data sources give different total global areas of coral reefs, based on their classification scheme and other factors. Here specifically, the use of the WCMC data then means that the total area of hard reef classes was statistically overestimated by a factor of 2.5 by the WCMC, while the total areas of soft reef classes was statistically underestimated by a factor 0.5, at least in 2006, though it is not clear whether this situation has improved (Andréfouët et al. 2006). These over and underestimations arise from the fact that the WCMC compiled global reef data from a variety of sources with different scales which lead to geolocation issues and errors of omission (Andréfouët et al. 2006). Future studies conducting similar research may wish to employ the use of more statistically accurate datasets such as, the Millennium Coral Reef Mapping Project which uses LANDSAT satellite imagery to precisely catalogue the global surface area covered by reefs (Andréfouët et al. 2006) and may have fewer data limitations. This data is freely available as raster or shapefiles, which are divided by Landsat scene or regional location which may prove useful for the analysis of individual reefs or reef locations (Andréfouët et al. 2006). However, using these various regional tiles on a global scale would have require a lot of spatial overlapping and so in the interest of time and efficiency, I chose, for the purpose of my study, to use the single, global UNEP-WCMC et al., (2021) dataset.

## *Conclusion*

This study examined the effects that increasing SST and surface ocean pH will have on the environmental suitability of the global ocean for existing shallow-water coral reefs by the end of the century, and implications for MPA protection of reefs and their biodiversity. These results, and how MPA coverage changes based on IUCN categories, can help to inform future conservation and management priorities for coral reefs in the face of climate change. Particularly striking was that 95.4% of total coral reef area was projected to be beyond SST and pH thresholds by 2090-2100 under a high-emissions scenario, with the total area of existing coral reefs protected by MPAs estimated to decline by 91%. However, the benefits of mitigation were also pronounced, with XXX% remaining in suitable habitat and YYY coverage by MPAs. Coral reefs are important ecosystems both in terms of their biodiversity and their provision of socio-economic goods and services (Hughes et al. 2017). Prioritizing effective coral reef conservation and management under the threat of climate change remains both crucial and challenging, with drastic losses in area of suitable habitat without serious attempts at climate change mitigation.

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