Climate-smart, 3-D protected areas in the high seas

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Abstract

Marine species are moving rapidly in response to warming, often in different directions and with variations by location and depth. This poses challenges to conventional reserve design. We develop a three-dimensional planning approach for the high seas that conserves biodiversity, minimises exposure to climate change, retains species within reserve boundaries, and reduces fishing conflict. Resultant climate-smart networks cover 11% of the high seas (5% of the ocean) and represent low-regret conservation options that are the first places to designate as new high-seas marine reserves. With the current push to increase the area of ocean under protection to 30%, we must confront the challenges of climate-smart three-dimensional conservation in the 41% of the ocean that is beyond countries' jurisdictions.

Main Text

Human threats – including fishing and climate change – are impacting marine biodiversity from the ocean surface to the deepest and most remote places on Earth[1,2]. Marine protected areas (MPAs) are the most effective and widely-used tools in conservation to mitigate effects of these stressors[3,4]. Well-enforced MPAs can protect biodiversity[5], enhance ecological resilience[6], and provide scientific reference sites in modified seascapes[7,8]. Of the few global MPA networks that have been proposed to safeguard marine biodiversity[9] and protect intact ecosystems by excluding anthropogenic threats[10], the only one to consider climate change in its design focuses on coastal waters[11].

Ensuring that MPAs are climate-smart (i.e., they are exposed to minimal climate threats) is challenging[12–14]. As the climate warms, species are rapidly shifting towards cooler regions[15–17], potentially moving beyond MPA boundaries. The retention of species in MPAs is further complicated by the three-dimensional nature of the open ocean, with the speed and direction of species' movement likely to vary with depth, a phenomenon that will be more pronounced in future[18]. As MPAs have largely been designed and applied in coastal and shelf regions, with no explicit consideration of different ocean depth zones, a new paradigm for the design of MPAs in the open ocean[19,20] is needed[21] – one that considers both its three-dimensional nature and climate change.

The high seas (i.e., the 61% of the ocean beyond national jurisdiction) are likely to be a primary focus of marine conservation in the future. While 17% of national waters in Exclusive Economic Zones (EEZs) are in MPAs, only 1.2% of the high seas is protected. This shortfall in the protection of the high seas means that currently only ~7.5% of the ocean is within MPAs[22], well short of the goal of protecting 10% of the ocean by 2020 set out in Aichi Target 11 by the Convention on Biological Diversity. Further, momentum is growing under the Post-2020 Global Biodiversity Framework to increase protection targets to 30% of the ocean by 2030[23]. Since the inception of protection goals, policymakers have known that they would need to use the high seas to meet marine targets, but have been hindered by fragmented governance regimes and the absence of global mechanisms to implement MPAs in the high seas[24]. The imminent agreement of a new treaty for the conservation and sustainable use of biodiversity beyond national jurisdiction will

establish just such a mechanism[22], finally providing an opportunity for policymakers to address the biggest gap in biodiversity protection on the planet.

To inform the development of MPAs in the high seas, here we develop a climate-smart planning approach that prioritises the conservation of global marine biodiversity across different ocean layers whilst minimising impacts to the fishing industry. We ensured MPA networks were climate-smart across three depth zones by identifying areas where biodiversity is more likely to be retained and have lower exposure to climate change. As a metric of retention, we used climate velocity[15], a generic predictor of the expected speed of species' distribution shifts if tracking climate[25,26]. Areas with slowest velocities are likely to see smallest range shifts. As a metric of Relative Climate Exposure (RCE), we used the temporal rate of temperature change divided by the mean annual temperature range (see Methods). This assumes that species exposed to slower warming and larger annual temperature ranges (i.e., where RCE is small) will be more resilient to climate change. We have focused on temperature in our analysis because of its fundamental importance as a driver of species' distributions[27], but other climate-change variables such as pH or oxygen concentration could be included[28]. We created spatial plans for three alternative futures based on ocean temperatures from the IPCC shared socioeconomic pathways (SSPs): SSP1-2.6 (an optimistic scenario with an emissions peak in 2020), SSP2-4.5 (an intermediate scenario with an emissions peak in 2040) and SSP5-8.5 (an unrestrained emissions scenario). Both climate-smart metrics were estimated globally across a 0.5°´0.5° grid in three depth layers: epipelagic (0-200 m), mesopelagic (200-1,000 m) and bathyabyssopelagic (>1,000 m). While governance of areas beyond national jurisdiction are divided between the water column and the seafloor, we limited our approach to the water column and pelagic fisheries, although it could be extended to include the seafloor in the future. Each spatial plan included a set proportion (see Methods) of the distribution of 11,701 species of vertebrates (fish, birds, mammals and reptiles), invertebrates (molluscs, arthropods and corals) and macroalgae (green, red and brown). As high-seas fisheries are a key economic resource[29], we minimised the cost to fishing, defined as the product of fish catch[30] and its price[31] at any point in space (see Methods). We used integer linear programming to identify priority areas for conservation for each depth layer and climate scenario using the R package *prioritizr*[32]. Our intent is to answer one pressing conservation question: can we identify climate-smart areas common to all future climate scenarios and across ocean depth layers? We argue that these are areas that should be targeted for urgent protection.

When we apply a climate-smart planning approach independently within each depth zone, there is moderate to substantial agreement among configurations of climate-smart MPA networks across emission scenarios in the epipelagic (, the mesopelagic ( ) and the bathyabyssopelagic ( ) zones (Fig. 1). This high degree of spatial correspondence implies that climate-smart conservation networks for particular depth zones could be robust to different climate futures. Given that we do not know the future climate, having substantial agreement among climate scenarios at each depth will be key to successful climate-smart conservation, and could maximise the protection of biodiversity.

Priority areas common across emissions scenarios could be considered “low-regret conservation areas”. Representing substantial proportions of the mesopelagic (44%), bathyabyssopelagic (37%), and epipelagic layers (34%) high-seas regions (Fig. 2, Table 1, Supplementary Table 1), these low-regret areas for conservation contain representative selections of oceanic biodiversity that is likely to be both retained within these areas and exposed to less warming. Therefore, if future conservation planning in the high seas were to focus solely on one of these depths, large areas would qualify for climate-smart protection. However, in a warming ocean, networks of vertically coherent MPAs across ocean depths would be the easiest to enforce and implement[18,28], raising the question of whether these low-regret conservation areas coincide across depth layers.

Identifying vertically coherent low-regret areas for protection is challenging because costs differ among depth layers (Extended Data Fig. 1a-c) and because the threat posed by disparate warming futures varies across depths (Extended Data Fig. 2-3). For example, future climate velocity is projected to be faster in the mesopelagic layer than in the epipelagic layer, even with strong mitigation of future emissions[15] (Extended Data Fig. 2). This could cause dissociation of bioregions across depths and compromise the functioning, effectiveness and ecosystem services of climate-uninformed MPAs. The RCE metric developed here shows a similar pattern: greater exposure to warming for species living below the epipelagic layers and under the SSP5-8.5 climate scenario (Extended Data Fig. 3).

This variability among depth layers means that climate-smart MPA network configurations exhibit more spatial agreement between epipelagic and mesopelagic zones (across emission scenarios) and between mesopelagic and bathyabyssopelagic zones ( ) than between epipelagic and bathyabyssopelagic zones ( ) (Fig. 1). Such spatial agreement in networks across depth layers reflects not only the similar lost opportunity cost to fishing (Extended Data Fig. 1d-f), but also the vertical coherence in the penetration of physical structures across depth zones, the vertical coherence of biodiversity through active vertical migration, and the passive transport of carbon via sinking production, particularly in the epipelagic and mesopelagic[33]. The lower coherence between the bathyabyssopelagic and the surface layer is unsurprising, given that many species are unique to the bathyabyssopelagic[34] and few vertically migrate the vast distances required to reach the epipelagic zone. The spatial coherence in the placement of MPAs in the epipelagic and mesopelagic zones is encouraging in terms of establishing climate-smart vertically-coherent MPAs, but the lack of coherence with the bathyabyssopelagic suggests that some separate zoning for the deep ocean might be needed.

The protection of ocean layers that are vertically coherent should be a priority in marine conservation planning. Our results show that 11% of the high seas are comprised of such “low-regret conservation areas” (Fig. 2d, Supplementary Table 1). These are ocean areas that are climate-smart across depths and climate futures, and that contribute to meeting our conservation targets whilst minimising fishing costs (Fig. 2, Extended Data Fig. 5). They represent the best places to conserve pelagic biodiversity in the high seas now and into the future (Extended Data Fig. 4-5). Importantly, in addition to the 11% of the high seas representing low-regret conservation areas across all depths, there is an additional overlap of “low-regret conservation areas” among pairs of depth layers. This overlap is more pronounced between contiguous

planning units in the epipelagic-mesopelagic (10% of the high seas) and mesopelagic-bathyabyssopelagic (11%) than between the epipelagic and bathyabyssopelagic layers (5%) (Fig. 2e, Supplementary Table 1). These areas may be useful when considering sectoral management measures that are largely restricted to specific depths, and might inform the development of other effective area-based conservation measures.

Conservation targets are a key component of conservation policy, but to date there has been more politics and expediency than ecology in how they are set in both global prioritisation exercises[10,35] and international policy arenas. To understand how species representation targets might alter the global climate-smart MPA network identified here, we created several climate-smart MPA networks with varying conservation targets for each conservation feature (see Methods, sensitivity analysis section). We find that when the area-based conservation targets were set low, the total area required to achieve those targets in each climate-smart MPA network was also low (Supplementary Table 1). Networks of vertically coherent low-regret conservation areas show a similar pattern, with less prioritised area for the 10–30% area-based target (0.76% of the total high seas) and more prioritised area for the 10–90% area-based target (6.47% of the total high seas) (Supplementary Table 1). Importantly, when varying targets for protection, there is still considerable spatial agreement among prioritised climate-smart networks across climate scenarios, and more spatial agreement in configurations between epipelagic and mesopelagic zones than between epipelagic and bathyabyssopelagic zones (Extended Data Fig. 7). Higher targets in a climate-smart prioritisation would increase “low-regret conservation areas” not only across different climatic scenarios, but also in a coherent way across depths. This can provide substantial benefits to the CBD agenda in a warming world.

A key assumption in our analyses is that the fishing cost layer by depth is accurate, because the prioritisation routine attempts to meet conservation targets whilst minimising cost. In this sense, the use of fishing as an opportunity cost layer (Extended Data Fig. 1a-c) is a global approximation of avoided conflicts associated with current fisheries (but see Caveat section in Methods). This layer could be improved as more data become available, especially for the deep ocean[36]. For instance, the number of mining licences to explore the deep-ocean seafloor is increasing[37], and this information could be incorporated in future analyses. However, one of the biggest issues of using a cost layer across ocean depths is that most of the information related to potential threats in the deep ocean is proprietary and unavailable to public scrutiny[38,39]. Therefore, international cooperation is vital to generate open-access information that can be used to minimise political and socioeconomic conflicts in the design of open-ocean climate-smart MPAs.

Designed and enforced appropriately, a global network of climate-smart MPAs in areas beyond national jurisdiction will help conserve marine biodiversity in a warming world. As we expand the global MPA network, we cannot ignore climate change or the complexities of conservation in three-dimensions. Our approach suggests several practical strategies that can support the expansion of MPAs, globally. The first priority should be the protection of the identified low-regret areas across ocean depths (11% of the high seas) as they are vertically coherent and robust to different climate futures. This would increase the

coverage of the global MPA network from ~7.5% to 15.5%. However, to meet higher global targets, society might need to consider separate reserve networks for different ocean depths, if they are to be robust to different climate futures. Since the climate-smart low-regret areas are geographically similar between epipelagic and mesopelagic layers, a second priority could be to focus on development of sectoral spatial management measures in the top 1,000 m of the ocean; this could add up to an additional 10% of the high seas as other effective area-based conservation measures that can be counted toward protection targets, bringing the global network under protection to 20% of the ocean. Doing so could also allow a greater focus on a separate planning process for the bathyabyssopelagic and the seafloor, which would need to consider potential costs beyond deep-sea fishing, including mining and cabling[38]. Last, given that our analysis has highlighted individual climate-smart MPAs and has not explicitly considered connectivity (see Caveats section), expansion in the global MPA network could further be realised through stepping-stone and mobile MPAs. Such climate-connected MPAs would enable biodiversity to shift along climate pathways[40].

As momentum builds towards protection of 30% of the ocean by 2030[23], the expansion of the current MPA network is a primary goal of the 2021-2030 Decade of Ocean Science for Sustainable Development. To be effective, conservation and management will need to include the high seas. We hope that the three-dimensional, climate-smart approach developed here will help inform MPA negotiations amongst member states and provide a robust blueprint for future spatial planning studies.

Methods

1. Study domain

We used the most-recent global marine regions dataset to define the spatial extent of the high seas (v11, https://www.marineregions.org/). We defined the high seas as marine areas outside of EEZs, which represent 95% of habitat on Earth by volume, 65% of the surface of the ocean, and 46% of the surface of the Earth[22]. We classified the high seas into three depth layers using the ETOPO1 bathymetry dataset[41]: epipelagic (0–200 m), mesopelagic (200–1,000 m) and bathyabyssopelagic (>1,000 m). We treated each depth layer as a separate planning domain. For every planning domain, we created an equal-area hexagonal grid of planning units of 2,620 km^2 (~0.5° at the equator). This yielded a total of 90,065 planning units for the epipelagic planning domain, 88,528 planning units for the mesopelagic planning domain, and 87,170 planning units for the bathyabyssopelagic planning domain; there are fewer planning units by depth because of seamounts and underwater mountain ranges. Information about climate metrics, species, and fishing data were assigned to each planning domain (described below), each of which could be prioritised for inclusion in a climate-smart MPA network.

2. Climate change metrics: sources and processing

Climate-change metrics (i.e., climate velocity and the relative climate exposure index) were estimated using future ocean temperatures from a multi-model ensemble mean derived from 11 general circulation

models (GCMs) from the Coupled Model Intercomparison Project Phase 6 (Earth System Grid Federation, https://esgf.llnl.gov; see Supplementary Table 2). We used models under three IPCC Shared Socioeconomic Pathways (SSPs)[42]: SSP1-2.6, SSP2-4.5 and SSP5-8.5. Pathway SSP1-2.6 represents an optimistic scenario, characterised by a shift to a more sustainable economy and reduction in inequality resulting in a peak in radiative forcing of ~3 W m^{-2} before 2100. SSP2-4.5 represents an intermediate scenario, with a stabilisation of radiative forcing levels at ~4.5 W m^{-2} by 2100. SSP5-8.5 is characterised by a continued increase of greenhouse gas emissions resulting from a fossil-fuel-based economy and increased energy demand, with a radiative forcing >8.5 W m^{-2} by 2100, rising thereafter.

For construction of the multi-model ensemble, we followed published methods[18]. Briefly, for each of the 11 climate models, we re-gridded from the original grid to a uniform 0.5° spatial grid using an area-weighted bilinear interpolation[43]. Then, we extracted depths according to three different ocean layers: epipelagic (0–200 m), mesopelagic (200–1,000 m) and bathyabyssopelagic (>1,000 m)[44]. For each depth layer, we averaged temperatures using a volume-weighting approach, with volumes of 0.5° grid squares in each depth layer. Finally, to avoid artefacts caused by inconsistent numbers of grid cells available by depth for different models, we included only grid cells common to all models within each depth layer[18]. All analysis was undertaken using software tools Climate Data Operators[45] and R[46] (Supplementary Table 2).

3. Climate velocity and the relative climate exposure metric calculations

To prioritise a climate-smart MPA network, we focused on areas across ocean depth layers that accomplish two objectives: 1) high retention of biodiversity, and 2) low levels of exposure to future climate warming. We used two metrics of climate change to represent these objectives: climate velocity and a Relative Climate-Exposure (RCE) index. Climate velocity is a metric that gives expectations for species' range shifts under projected future ocean warming[15,25]. Thus, it is expected that in areas of slow climate velocity, species' distributions are likely to shift less, promoting their retention within a given area. We estimate local climate velocity at 0.5° resolution for the second half of the century (2050–2100) at each ocean depth layer of the multi-model CMIP6 ensemble. The temporal trend (i.e., numerator of climate velocity) was calculated as the slope of a linear regression of mean annual temperatures (°C yr^{-1}) for the corresponding climate scenario time period. The spatial gradient (i.e., denominator of climate velocity) was calculated from the vector sum of the latitudinal and longitudinal pairwise differences of the mean temperature across the corresponding climate scenario and time period at each focal cell using a 3×3 neighbourhood window (°C km^{-1})[15]. All calculations were performed using the VoCC R package[47].

RCE is a metric we developed to obtain information about the amount of exposure to climate warming that local populations of a species would face relative to its experience of variation in seasonal temperatures. We calculated RCE as the ratio of the slope of a linear regression of projected mean annual temperatures (°C yr^{-1} 2050–2100) to the current mean seasonal temperature range (°C from 2015–2020):

$$\text{RCE (Relative climate exposure)} = \frac{\text{Slope of temperature change (°C yr}^{-1}\text{)}}{\text{Current seasonal range (°C)}}$$

Therefore, it is expected that by prioritising areas with a low climate-exposure index we will select MPAs that will be more likely to minimise the potential exposure of species to future warming. Although some metrics of exposure have been already incorporated in marine spatial planning[48–50], our metric considers not only information on warming, but also the relative local change relative to seasonal variation, and therefore, presumably, the relative vulnerability of resident biodiversity to projected future temperatures. For each planning unit in each depth domain, we calculated climate velocity and RCE separately for all three SSPs.

4. Conservation features

To solve the minimum-set conservation prioritisation problem, it is necessary to set a protection target *a priori* for each conservation feature, which indicates the minimum amount of each feature (i.e., species, habitat) to be included within the final prioritised network[51]. Here, our conservation features were marine species distribution maps from AquaMaps[52] (v2019). The AquaMaps dataset predicts marine species distributions using a probability of occurrence (0–1) derived from an environmental niche model based on depth, temperature, salinity and oxygen at 0.5° spatial resolution. It includes 33,518 marine species, 23,700 of which we considered, as their environmental envelopes were generated using at least 10 observations [18,53]. We used a minimum threshold of 0.5 probability of occurrence to select range maps for our high seas planning region as a conservative threshold defining core distribution ranges of the species[10,18,53]. Since most biodiversity in the ocean is located in coastal regions, our selection criteria yielded 11,701 species distribution maps in the high seas planning region (Supplementary Table 3).

We assigned each species distribution to each depth layer planning domain based on the species' depth range derived from AquaMaps depth envelopes. This yielded a total of 8,538 conservation features in the epipelagic planning domain (0-200 m), 4,329 conservation features in the mesopelagic planning domain (200–1,000 m), and 1,472 conservation features in the bathyabyssopelagic planning domain (>1,000 m) (Extended Data Fig. 1d-f, Supplementary Table 3).

To obtain a better representation of conservation features in the global climate-smart MPA network across latitudes and ocean depth layers, we ensure that each is represented in every marine biogeographical province that it overlaps with. We used different biogeographical provinces for different depth layers. For the epipelagic planning domain, we used Longhurst Provinces[54] and for the mesopelagic and bathyabyssopelagic planning domains, we used Glasgow Provinces[55]. Since most conservation features appear in multiple provinces, this categorisation process yielded a total of 56,996 conservation features: 19,761 for the epipelagic planning domain, 23,360 for the mesopelagic planning domain, and 13,875 for the bathyabyssopelagic planning domain.

5. Opportunity cost of fishing

When solving the minimum-set problem in spatial prioritisation, the objective is to identify areas where MPAs can meet conservation targets at a minimum cost. In our global prioritisation analysis, we used the value of fisheries as a cost layer because it is most common cost layer used in marine planning as resulting priority areas avoid valuable fishing grounds, where possible[56]. To estimate the cost ($US) of each planning unit in each depth layer planning domain, we multiplied an estimate of the total catch (kg) by the price per kg for each species caught ($US kg^{-1}). The data were obtained from the Sea Around Us project dataset, which compiled fishing records for 1,242 species of fish and invertebrates from different publicly available databases from 1950-2014[30]. This dataset includes landings at 0.5° spatial resolution, it is interpolated to account for missing values, and includes an estimate of illegal, unreported and unregulated fishing recorded as discards[30]. We calculated the total catch from 2005–2014 in each 0.5° cell (Extended Data Fig. 1a-c) and obtained the mean price of each species ($US)[31]. We then used the FishBase database (https://www.fishbase.se/) to categorise each species by depth (minimum and maximum preferences). This yielded a total of 1,099 prices for species ($US), 669 prices for the epipelagic layer, 322 prices for the mesopelagic layer and 118 prices for the bathyabyssopelagic layer. To obtain a final cost layer for each ocean depth layer, we calculated a total price by adding prices for every species within each 0.5° cell. We overlapped each cost layer generated with the corresponding high seas depth layer planning domain to obtain an area-weighted mean total cost ($US) for each planning unit (Extended Data Fig. 1a-c).

6. Spatial conservation prioritisation

We used integer linear programming (ILP) to find climate-smart MPA networks across ocean depth layers that minimise the overall cost (i.e., fishing value, US dollars) of the MPA network, and achieve the representation targets for each conservation feature. We solved the minimum-set objective[51] using the *Prioritizr* R package[32] and Gurobi optimisation software[57]. We set Gurobi to achieve a solution within 10% of the optimal solution. This is a relative arbitrary number that establishes the difference between the upper and lower bounds of the objective function[58]. For example, a value of 0.10 will result in the optimizer stopping and returning solutions when the difference between the bounds reaches 10% of the upper bound. The optimal solution is that which achieves the coverage target with the lowest possible cost.

Targets for conservation features were generated as follows (Extended Data Fig. 6). First, each conservation feature was intersected with both climate velocity and RCE maps to obtain its corresponding climate-change condition in each planning unit. Then, for each conservation feature, we selected only the planning units in which the conservation feature experienced slow climate change. We defined a slow climate change as values in the lowest quartile for each climate velocity and RCE metric (i.e., slow climate velocity and low RCE) within the range of the species under consideration (Extended Data Fig. 6). This process reduced the distribution size of each conservation feature (i.e., number of cells represented in the high seas) to one quarter of its initial distribution (Extended Data Fig. 6), yielding

“restricted” conservation features. Next, for each of these restricted conservation features, we assigned targets based on the conservation status reported by the IUCN Red List[59]. For this, we used the *rredlist* R package[60] to obtain the IUCN classification for each conservation feature. For taxa reported as threatened (i.e., VU = vulnerable, EN = endangered, or CR = critically endangered), every associated restricted conservation feature was assigned a fixed target of a 100%[10] (i.e., 100% of its distribution within the first quartile of our climate-smart metrics for its overall distributional range) (Extended Data Fig. 6). For conservation features not reported as threatened in the IUCN Red List, we assigned relative targets based on the size of its global distribution (i.e., the restricted conservation feature) represented in each ocean depth planning domain, with a minimum of 10% for features with broad ranges, and 100% for features with limited ranges (10–100% of its restricted distribution for each conservation feature) (Extended Data Fig. 6, see Sensitivity Analysis section). We calculated these relative targets following the equation:

$$\text{Target (\%)} = \text{Target}_{max}\ (\%) \times \frac{\text{PUs}_i}{\text{PUs}_{total}} \times (\text{Target}_{max}\ (\%) - \text{Target}_{min}\ (\%))$$

where Target_{max} and Target_{min} refer to the maximum and minimum target of protection (%) for restricted conservation feature *i*, $\text{PUs}_{(i)}$ represents the number of planning units represented for slow conservation feature *i*, and PUs_{total} refers to the total number of planning units for each high-seas depth planning region. By using relative targets instead of fixed targets, we ensured both the representation of multiple areas where widely-distributed restricted conservation features were conserved, as well as the protection of restricted conservation features within limited distribution ranges[10].

We created different prioritisation planning scenarios to determine how the incorporation of climate-change metrics (i.e., slow climate velocity and low RCE) drives the selection of a climate-smart MPA network under alternative climatic futures. We ran three scenarios: one where we included restricted conservation features under SSP1-2.6; one with restricted conservation features under SSP2-4.5; and one with restricted conservation features under SSP5-8.5. Each prioritisation scenario locked in protection in existing MPAs (data extracted from www.protectedplanet.net) and Vulnerable Marine Ecosystems (VMEs, data extracted from www.fao.org).

To determine the spatial similarity of selected planning units among prioritisation scenarios and ocean depth planning domains, we calculated the Cohen’s Kappa coefficient. Cohen’s Kappa is a pairwise statistic that indicates the degree of agreement among scenarios, ranging from -1 to 1, where -1 represents complete disagreement, 0 represents agreement due to chance, and 1 represents complete agreement[61].

7. Sensitivity analyses

The total area protected in a prioritisation analysis is highly correlated with the initial target assigned to each conservation feature. To test the sensitivity of our analysis to each conservation feature, we tested different targets of protection for the climate-smart prioritisation planning approach, with a minimum of 10% and adding 10% to a maximum of 90% (10–90% of the restricted distribution for each conservation feature). This gave a total of seven new and different planning scenarios (Supplementary Table 1). For each set of targets (i.e., planning scenarios), we performed a prioritisation analysis using the *Prioritizr* R package and the Gurobi software. As in the main design, we set Gurobi to achieve a solution within 10% of the optimum solution.

8. Caveats

There are several key sources of uncertainty in the current study. First, the climate-smart prioritisation planning approach taken to the conservation of individual species in this study assumes that every cell considered habitat in the AquaMaps dataset is of equal value. Scaled up, this implies conservation of any area-based target of a species distribution confers equal protection for the species. Recent analyses made the same assumption[62] because these distributions are the best available data we have that cover the geographic and taxonomic scope of these studies. However, this approach does not take into account metapopulation structure, life-history, or how a population uses different habitat patches (e.g., for breeding, foraging, or migrating). It is clear that all parts of a species' range are not equally important and that conserving any target for a species range will not necessarily confer the protection necessary to conserve metapopulation structure or even the species as a whole. We strongly encourage further research to improve our understanding of how species use and connect across the ocean, and the incorporation of this knowledge to improve global species distribution models like AquaMaps.

Second, our climate-smart prioritisation planning approach did not consider the three main aspects of a well-connected marine MPA network in its design[63] (i.e., structural connectivity, functional connectivity, climate connectivity) and only represents the most cost-efficient climate-smart solution in a global scale analysis – meeting all the proposed conservation feature targets by minimising the fishing cost. But connectivity in the marine realm might be even more challenging to address, especially considering the three-dimensional nature of the ocean. This would require consideration of horizontal and vertical connectivity within and across ocean layers. These aspects were beyond the scope of this study but could be considered in further research. Third, there are limitations associated with the static cost layer of current fish prices in our analysis. The main objective of this study is to identify current climate-smart areas that will retain biodiversity and be least exposed to climate change to proactively plan for long-term ocean protection[64]. However, the cost layer used could also change as a result of changes in climate velocity and RCE which can derive in changes in the global distributions of fishes as the climate warms. Incorporating dynamic conservation features and cost layers using projections for biodiversity and fisheries could be a promising way forward for future research.

In this study, there is uncertainty associated with the climate models used to estimate the climate velocity and RCE. Although CMIP6 GCMs models have finer spatial resolution than CMIP5 models for both

horizontal and vertical grid cells, uncertainty can still vary with depth[18]. These uncertainties might also generate differences in estimates of climate velocity and RCE metrics . This is an important consideration, especially for climate-smart planning approaches that rely on climate-change projections.

Finally, both climate velocity and RCE are generic metrics that do not directly link climate warming with species' thermal preference. The RCE metric developed here indirectly relates vulnerability of marine biodiversity to climate warming (i.e., how sensitive they are to that level of exposure), but the analyses might be strengthened by better linking the hazard (i.e., climate warming), the exposure to that hazard (the amount of warming at the spatial unit of analysis), and the vulnerability of local marine communities to that hazard (how sensitive they are to that level of exposure). Again, these aspects were beyond the scope of the current study that included thousands of marine species, but could be considered in further research, should such data become available.

Declarations

Data availability

All data are available at The University of Queensland's eSpace: https://doi.org/10.14264/34d915e. Correspondence and requests for materials should be addressed to I.B.M (i.britomorales@uq.edu.au).

Code availability

Scripts are available at The University of Queensland's eSpace: https://doi.org/10.14264/34d915e.

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Author Contributions

I.B.M., D.S.S. and A.J.R. conceived the research. J.D.E. generated the fishing cost layer. I.B.M analysed the data. I.B.M wrote the first draft with inputs from D.S.S., A.J.R. and C.J.K. I.B.M., D.S.S., A.J.R., C.J.K., D.C.D., J.D.E., J.G.M., M.T.B., R.M.D., H.P.P. contributed equally to discussion of ideas and analyses, and all authors commented on the manuscript.

Competing interests

The authors declare no competing interests.

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Tables

Table 1. Proportion of the high seas (%) covered by all slow conservation feature priorities under different climate scenarios.

Ocean layer planning domain	SSP1-2.6	SSP2-4.5	SSP5-8.5	Climate-smart network (all three SSPs)
Epipelagic (0 – 200 m)	53	56.3	57.4	33.8
Mesopelagic (200 – 1,000 m)	59.3	58.8	59.5	44.02
Bathyabyssopelagic (>1,000 m)	52.4	50.4	49.7	36.71
Vertical climate–smart network (all three planning domains)	-	-	-	11%

Figures

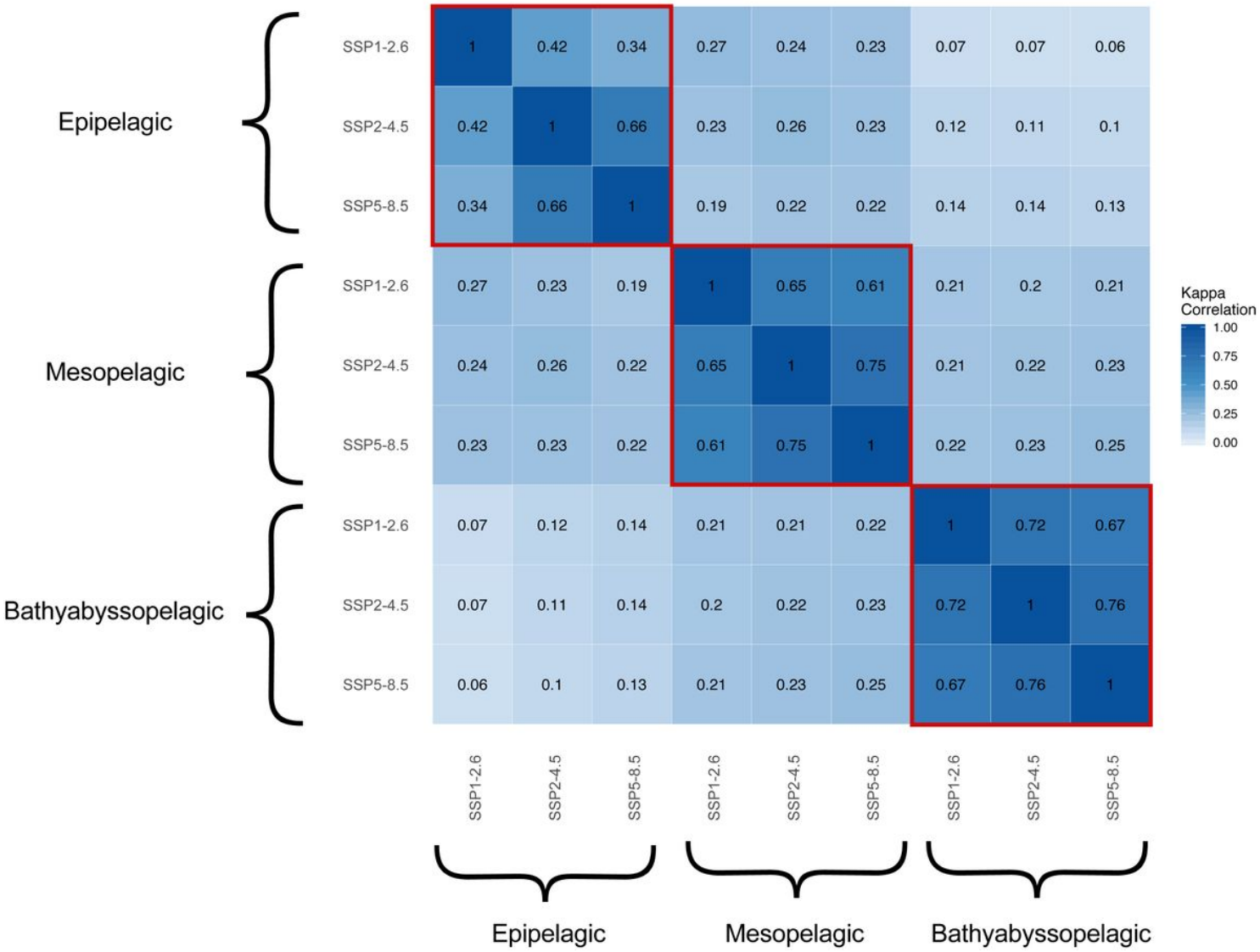

Figure 1

Kappa correlation index for the relationship between each prioritised climate-smart network design for three ocean depth layers.

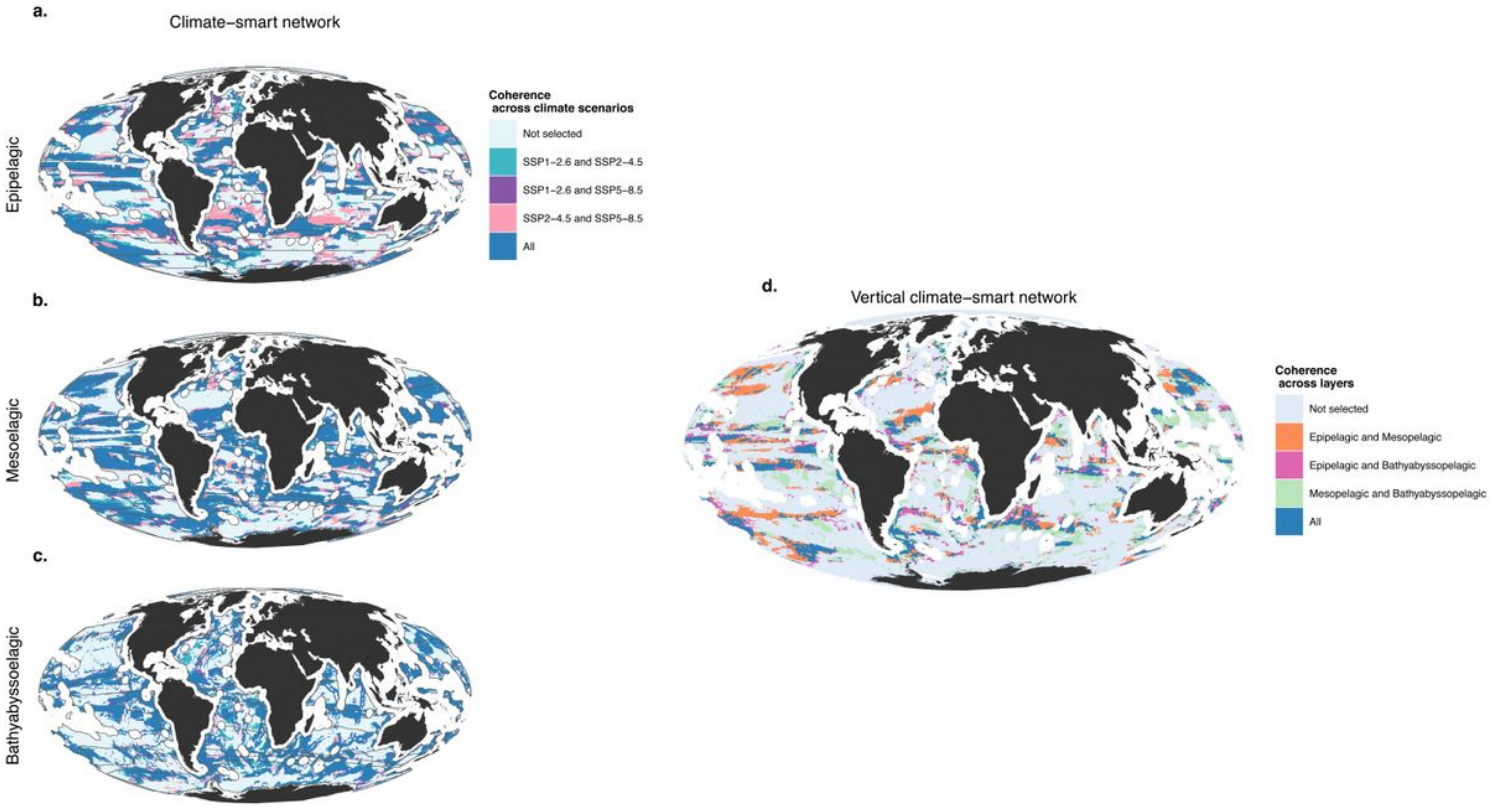

Figure 2

Coherence of prioritised networks in the high seas across three depth zones and three climate emissions scenarios. Climate-smart prioritisation networks as low-regret conservation areas for: a. Epipelagic, b. Mesopelagic, c. Bathyabyssopelagic, and d. throughout the water column of the ocean under three IPCC Shared Socioeconomic Pathways: SSP1-2.6, SSP2-4.5, and SSP5-8.5. Polygons represent Longhurst provinces for the epipelagic layer (a.) and Glasgow provinces for the mesopelagic (b.) and bathyabyssopelagic layers (c.).

Supplementary Files

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- BritoMoralesetal.2021.SOM.docx
- ExtendedData.pdf