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Biogeographic constraints to marine conservation in a changing climate

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The siting of protected areas to achieve management and conservation objectives draws heavily on biogeographic concepts of the spatial distribution and connectivity of species. However, the marine protected area (MPA) literature rarely acknowledges how biogeographic theories underpin MPA and MPA network design. We review which theories from biogeography have been incorporated into marine spatial planning and which relevant concepts have yet to be translated to inform the next generation of design principles. This biogeographic perspective will only become more relevant as climate change amplifies these spatial and temporal dynamics, and as species begin to shift in and out of existing MPAs. The scale of climate velocities predicted for the 21st century dwarfs all but the largest MPAs currently in place, raising the possibility that in coming decades many MPAs will no longer contain the species or assemblages they were established to protect. We present a number of design elements that could improve the success of MPAs and MPA networks in light of biogeographic processes and climate change. Biogeographically informed MPA networks of the future may resemble the habitat corridors currently being considered for many terrestrial regions.

Keywords: connectivity; range shifts; conservation planning; marine reserves

Introduction

Marine conservation is an inherently spatial endeavor, whether explicitly, in the case of marine spatial planning, or implicitly, by virtue of the fact that any marine policy or management plan has a spatial jurisdiction. Thus, biogeography—the study of patterns and processes in the distributions of species—should be central to conservation planning. However, biogeography has rarely been explicitly applied to marine conservation. Here, we review the challenges facing the design of marine protected areas (MPAs)—the most widely recognized form of marine spatial conservation—in the 21st century and argue that broader use of the insights from existing biogeographic principles could substantially improve the design of MPAs in the future. MPAs are geographically delineated areas that are "designated or regulated and managed to achieve specific conservation objectives,"[1] acknowledging that MPAs that prohibit fishing (i.e., marine reserves) may be more

successful at achieving conservation objectives than mixed-use MPAs.[2]

MPA design research has primarily focused on small-scale ecological and social processes that impact the size and shape of individual MPAs or the connectivity and representation among a network of MPAs.[3] (Social and economic dimensions of MPA design, which are critical elements but fall beyond the scope of this review, have also received significant research attention.[4–6]) MPAs are typically established to achieve a set of goals related to biodiversity conservation and more recently for fisheries management.[7] Given their small-scale goals and typically small size, most single MPAs are unlikely to contribute significantly to the conservation outcomes of an entire species.[8] Recognition of this constraint has prompted calls for larger MPAs, MPA networks, and the integration of MPAs into ecosystem-based management.[8–10] As MPAs are gradually applied at larger spatial scales,[11] and as

climate change increases the possibility of local extinction within small MPAs, understanding and predicting species range limits and future range shifts is becoming increasingly important to MPA design.

The explicit application of biogeography to marine conservation has primarily focused on defining unique assemblages of species and setting conservation targets for those assemblages. These targets are commonly embodied in the conservation planning principles of representation (which guides MPA placement to include locations with representative examples of the full suite of species) and replication (which spreads risk among multiple MPAs within a biogeographic region).[12,13] Much less directly, MPA planning also borrows principles from biogeography when accounting for and modeling larval dispersal and connectivity, but rarely in a systematic way.[14] Other active areas of research in marine biogeography, such as within-range distributions of individuals within species, are rarely acknowledged in MPA-design research despite having the possibility to profoundly influence optimization models of MPAs and MPA networks, including the differential benefits of protecting different places within a species' range.[15,16] In general, research on MPA design tends to incorporate more sophisticated models of physical dynamics (e.g., advection-diffusion of currents, temperature, and pH) than of ecological dynamics (e.g., within-range species distributions, habitat associations, migrations and range shifts, species interactions, and adult movement).[7,17–20] However, ecological dynamics clearly affect the abundance and distribution of species over space and time, and thus possibly the success of MPAs in achieving diverse conservation goals. A clear example of where such dynamics are considered is with trophic cascades, where protection of top predators can have implications for the abundance and viability of prey species that may also be conservation targets.[21,22] Less dramatic but equally important predator–prey competition, facilitation, and other interactions are not typically accounted for in MPA design, yet they can profoundly affect the pace and ultimate outcome of conservation.[23]

Biogeography will become even more important to MPA design under climate change, which is predicted to cause rapid and heterogeneous changes in species distributions, with uncertainty in these changes among climate change scenarios.[24] Many factors will influence if or how species respond to climate change, most notably the regional intensity of climate change but also the pressures from other human activities.[25] Most existing studies on climate change and MPAs have suggested a focus on reducing cumulative impacts and/or building resilience within MPAs, and risk-spreading and buffering catastrophic events in MPA networks, as a way to mitigate climate impacts.[26–28] Missing from this literature is consideration of how biogeographic factors may alter species responses to climate change, and thus conservation strategies. Here, we contribute a biogeographic perspective to this literature by reviewing how MPAs have adopted biogeographic principles, which might be useful if better incorporated, and how biogeography can inform MPA planning under climate change. To inform these recommendations, we present a simple analysis of the spatial scale of most existing MPAs relative to species' range sizes and marine climate velocities from 1960 to 2009. We focus on large MPAs and MPA networks, which are relatively rare but becoming increasingly common and have outsize importance in marine conservation; there are 75 MPAs in the world that exceed 100,000 km^2 of protected oceans, while almost 14,000 MPAs exist under 100 km^2.[1]

How biogeography affects MPA success

The design of MPAs and MPA networks—i.e., their size, shape, location, and spacing—ultimately rests on principles adopted from biogeography. In the theory and application of MPAs, biogeography is commonly used to subdivide oceans into areas with relatively consistent and distinct habitats, flora, and fauna. These biogeographic "regions," "provinces," or "zones" are often used as boundaries for defining where and how to achieve representation and replication goals.[29,30] The most common tools used to design MPA networks—Zonation and Marxan—can be applied to achieve target levels of representation and replication, if provided with biogeographic information (i.e., the spatial extent of species and habitats).[31] Treating biogeographic representation and replication as a conservation target is considered the "best practice" for MPA network design and has been widely applied.[29,30]

However, marine conservation planning has not yet applied the major caveat of using these

biogeographic units: they can move on a variety of time scales.[32,33] MPA planners who make decisions based on biogeographic units rarely acknowledge that the edges of species distributions, which in aggregate define biogeographic provinces, can be quite dynamic. An MPA, or a network of MPAs, designed to represent a biogeographic province with replication might fail to do so if biotic and abiotic processes that drive range fluctuations are not considered.

Biogeography theory has also strongly influenced MPA design through aspects of the theory of island biogeography. Most notably, early MPA design models[34] made the extreme case assumption that habitats outside of MPAs had no populations, which is highly analogous to the equilibrium theory of island biogeography.[35,36] In that framework, populations are assumed to only persist within MPAs. Therefore, a patch model of MPAs where there is no adult survival or larval production outside of protected areas is effectively identical to a network of islands for terrestrial species.

As a discipline, biogeography has disproportionately focused on terrestrial systems, with quantitative and theory-driven marine biogeographic studies relatively rare.[37] More recently, marine biogeography has evolved rapidly, progressing far beyond simple models of immigration and extinction to shed light on complex dispersal processes, range dynamics, and connectivity in the sea.[38–43] Recent models of MPAs and MPA networks rely on metapopulation models, which in turn incorporate source-sink dynamics and persistence.[44–47] While the field of metapopulation dynamics is not considered a derivative of biogeography, it inevitably draws upon marine biogeographic principles regarding dispersal and connectivity when applied to spatially explicit scenarios such as MPA planning.

The treatment of dispersal in metapopulation models for MPA planning has become remarkably sophisticated,[30] but has historically lacked empirical data on larval dispersal for validation.[46] Several studies have attempted to ground-truth dispersal models with real data, primarily for tropical corals and reef fish.[48–50] These efforts to improve larval dispersal models are crucial for accurate and informed MPA planning. Unfortunately, less research exists on the spatial dynamics of adults, which can also inform metapopulation models, even for species that accomplish most of their movement as larvae.

The significance of adult spatial dynamics for mobile marine species is self-evident and has recently been incorporated into some metapopulation models.[7,20] However, within-range adult distributions of sessile species can also shed light on important dispersal processes and inform the design of MPAs.

Within-range dynamics of species, and the processes that establish range edges, have been an area of interest in biogeography for decades. In 1972, Robert MacArthur wrote that "patterns on islands, of species diversity, and of tropical communities are already clear and even moderately well understood, while patterns of single species' ranges still seem to be catalogs of special cases."[32] MacArthur and others wrote extensively on the role of climate, habitat, and species interactions in establishing range edges, but very little was known about how individuals are arrayed within the species range. The only generalizable ecological rule on the topic is the abundant-center hypothesis, which originated in the early 20th century with the work of Grinnell and others,[51] and predicts that a species' population density is highest at the geographic center and declines toward the range edges.[52,53] Unfortunately, the abundant-center hypothesis is not consistently supported by data, and no universal theory has emerged to replace it.[16,54] In the marine environment, it is not uncommon for coastal and intertidal invertebrates to be most abundant at one range edge, possibly because their distributions are mediated by oceanographic flow regimes.[41]

Analyses of MPAs that use real data on adult and larval distributions may be able to sidestep the theoretical debate regarding the drivers of range edges and within-range abundance. However, models of MPAs and MPA networks should critically examine their biogeographic assumptions, including whether the within-range distributions (i.e., spatial population matrices) used are justified. Even though the size of a species' range is rarely considered in conservation planning, a recent terrestrial study found that incorporating range size into an optimization model for conservation hotspots led to very different recommendations than using other targets such as species richness.[55] The identification of marine conservation hotspots might be similarly influenced by considering range size. Embracing this and other biogeographic perspectives on marine spatial planning will almost certainly lead to management recommendations that

are more realistic for the dynamic and complex oceans.

Biogeography and MPAs under a changing climate

Biogeography is devoted to understanding and modeling the spatial arrangement of individuals, populations, and species. These dynamics are applicable to all MPA-design processes, but they are unequivocally crucial for anticipating the influence of climate change on MPAs. Climate change is predicted to affect species via multiple pathways at numerous scales, including altered survivorship, growth, reproduction, spatial distributions, and species interactions.[56] Past reviews on MPAs and climate change have made qualitative recommendations to enhance resilience via risk-spreading and MPA connectivity.[26,27,57,58] However, they have rarely addressed whether species will persist in their current distributions and abundances, or at all—a fundamental question that must be answered as a precondition to MPA planning. Predicting the future state of species and communities protected by MPAs requires modeling both their distributions and persistence.

Persistence of populations is not widely incorporated into models of MPAs and networks, although literature on the topic is rapidly growing.[44–47] As described above, biogeographic theory on larval dispersal and source-sink dynamics clearly underpins this area of research on MPAs. These metapopulation models may inform the fine-scale siting of MPAs in the climate change context by predicting which habitats will be colonized by, and support persistent populations of, species that are shifting their ranges.

Modeling future species distributions has received intensive research effort in recent years, as global climate models have become widely available for use in ecology.[24,59] These models are becoming increasingly realistic with endeavors to incorporate species interactions, multiple climate variables, physiological responses, and other dimensions in addition to projected temperature changes.[60] Although biotic processes have been a recent focus of species distribution modeling, models of physical processes associated with climate change—such as thermal exposure that might lead to coral bleaching,[27] changing patterns in oceanic currents that could influence larval dispersal,[61] and effects of temperature on larval development times and dispersal distances[62]—are equally if not more sophisticated.

Indeed, distribution models using "climate velocity" (the rate and direction of thermal envelope shift predicted for a spatial cell) may have outstripped the empirical evidence for range shifts, which shows highly individualistic responses to 20th century warming, including species that do not shift their ranges at all or shift in an unexpected direction.[25,63,64] Given the multitude of biotic and abiotic processes that influence species range edges, it is unsurprising that temperature alone does not explain all of the observed variance in Anthropocene species distributions.[60] In the oceans, biogeographic processes—particularly biogeographic boundaries—may play a critical and overlooked role in mediating species' responses to climate change. Marine biogeographic boundaries often occur at major breaks in coastal currents, which inhibit larval dispersal in one or both directions along the coastline.[65,66] Due to their ability to influence dispersal, marine biogeographic boundaries may pose a particular concern for species that migrate in response to climate change. Biogeographic theory on larval dispersal can inform predictions of future species distributions and persistence, and thus improve forecasting for communities protected by MPAs.

Recommendations for improving MPA design

Recent efforts to evaluate the utility of MPAs in the 21st century frequently focus on building resilience and reducing cumulative impacts, which would in theory buffer the worst effects of climate change in the oceans.[28] However, there has been relatively little analysis of the spatial scales of important processes in MPA planning, despite widespread advocacy for larger and more connected MPAs. We provide a quantitative comparison of the scale of MPAs in contrast to climate velocities and species' ranges sizes, and provide novel recommendations for MPA design given their diminutive size relative to biogeographic processes.

We examine the size distribution of existing MPAs and MPA networks relative to marine climate velocities from 1960 to 2009 and projected range sizes of marine species (Fig. 1 and Supplementary online file). As a simplifying first approximation,
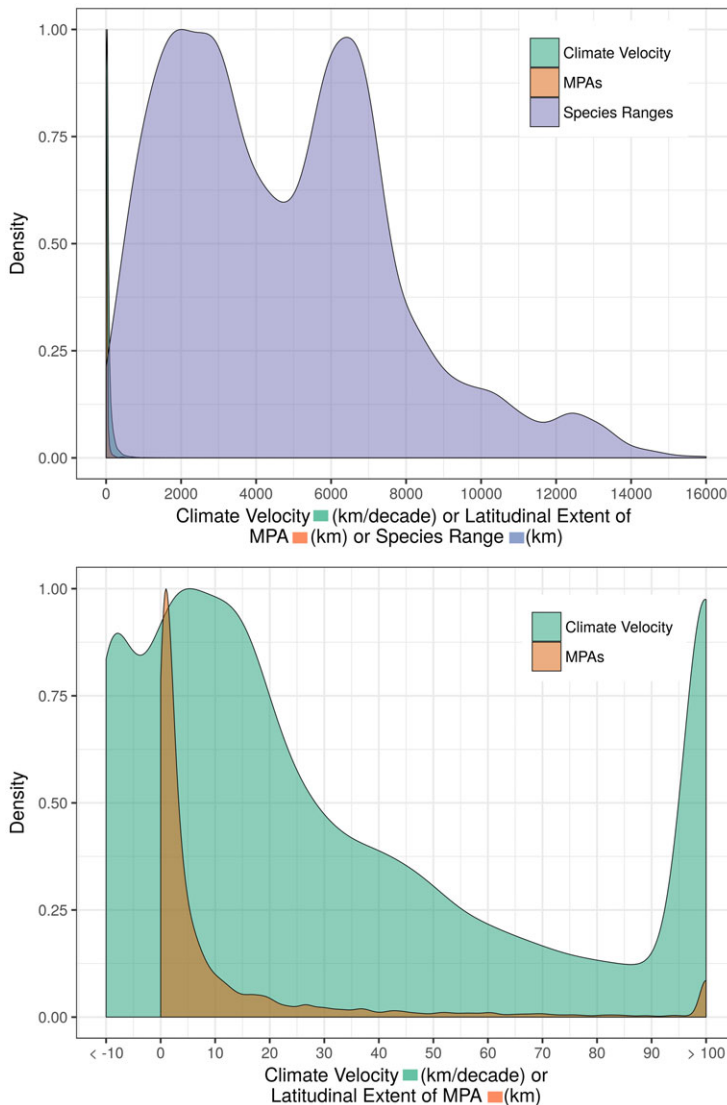
Figure 1. Spatial scale of MPAs (latitudinal (north-south) extent, $N = 5727$), marine fish species ranges (latitudinal (north-south) range extent, $N = 12{,}345$), and positive (warming) climate velocities of sea surface temperature from 1960 to 2009 ($N = 43{,}425$), displayed using a smoothed density function with the most frequent value scaled to 1 for each data series (A). Panel B shows fine-scale density distribution of MPA sizes and climate velocities, including negative (cooling) climate velocities; values greater than 100 km or km/decade and negative climate velocities (i.e., values beyond the *x*-axis bounds) were binned for visual purposes. Latitudinal extent of MPAs and MPA networks was extracted from the World Database of Protected Areas[1] (WDPAs) using only data on protected areas in IUCN protection classes I–IV (the stricter conservation classes that prohibit most extractive uses)[91] and using the WDPA classification of networks.[91] MPA latitudinal extent was calculated as the difference between the maximum and minimum latitude of a bounding box drawn around each MPA in the filtered list from the WDPA; each sample in the distribution plotted here is one MPA. Range data are based on Aquamaps predicted spatial distributions for cartilaginous and bony fishes,[92] with probabilities of occurrence below 60% excluded to be conservative. Range latitudinal extent was calculated as the difference between the maximum and minimum latitudes of spatial cells where a species' probability of occurrence was greater than or equal to 60%, measuring from the center of the half-degree square cells used in Aquamaps; each sample in the distribution plotted here is one marine bony or cartilaginous fish species' range. Climate velocity was calculated as "the ratio of the long-term temperature trend (in°C/year) to the two-dimensional spatial gradient in temperature (in°C/km, calculated over a 3°-by-3° grid), oriented along the spatial gradient"[59] and is presented in km/decade up to 16,000 km for 1°-by-1° cells in the global oceans based on 1960–2009 data (provided by M. Burrows); each sample plotted here is the climate velocity for one marine spatial cell.[59]

we only consider the latitudinal extent—i.e., "height"—of MPAs and species' ranges. Marine bony and cartilaginous fishes typically have very large geographic ranges, with a median range latitudinal extent of 4384 ± 2970 km (standard deviation). Climate velocities from 1960 to 2009 exceeded 200 km/decade in some areas, although many parts of the ocean surface had minimal temperature change during this period. However, the median latitudinal extent for MPAs is just 2.7 km—several orders of magnitude smaller than many range shifts already documented in the oceans.[67]

With the exception of MPAs that are either very large, in networks, or in places that are not warming rapidly, this scale mismatch suggests that many MPAs are at risk of losing the species they were originally established to protect. MPAs that were created to protect geomorphological units, habitats, or assemblages (e.g., coral reefs or seamounts) are still likely to be undermined by climate-related range shifts of individual species and the loss of the services they provision. Individual MPAs outside of networks, except in the rare cases of giant MPAs that approach the scale of a species' geographic range, appear unlikely to provide substantial benefits to an entire species. Although individual MPAs may certainly offer local benefits to populations and ecosystem function, most do not have the spatial extent necessary to protect an entire species (except endemics with tiny ranges) from the effects of climate change.

Given this scale mismatch, we offer the following recommendations for MPA design in the Anthropocene. First, while small MPAs are unlikely to contribute materially to species-level conservation, they can nonetheless have an outsized impact if sited with consideration of climate velocity and the range size of species of interest. For example, MPAs intended to protect single species that are sited closer to the leading (often poleward) edge of the geographic range will keep that species within their boundaries far longer than MPAs sited at the trailing (often equatorward) edge (Fig. 2A versus B). However, this approach is likely impractical for MPAs intended to protect diverse species assemblages, because each species has a different geographic range and range size, and tends to shift at different rates. In addition, given the scale of climate velocities (Fig. 1), almost no single fixed MPA can feasibly protect most marine species for decades and centuries to come.

Very large MPAs may achieve that goal, although they are exceedingly difficult to design and manage effectively.[68,69] Setting aside the complex political context of large MPAs,[70] our second set of recommendations address the siting and design of large MPAs should they be implemented. Many existing large MPAs are designed to be "wide" (e.g., the Mid-Atlantic Ridge North of the Azores), to cover habitats that occur at specific latitudes (e.g., reefs and seamounts), achieving replication and representation goals in the present but not necessarily protecting habitats that might be important in the future.[71] To protect future populations *in places where species are predicted to shift* (which may not be the case in tropical ecosystems such as coral reefs for which habitat is unavailable past certain latitudes), large MPAs should be designed as "tall" rather than "wide." This strategy would encompass more habitat that might continue to support species of interest in the future, based on climate velocity predictions (see design of MPA "chains," below). To cover 50% of the latitudinal extent of a median species range in our dataset, a large MPA would have to extend 4329 km in latitude, or approximately 39°. For reference, the Coral Sea Commonwealth Marine Reserve—one of the world's largest MPAs—covers 14.84° of latitude. Large MPAs should also be designed to encompass features with disproportionate conservation significance (Table 1), discussed in more detail below. In general, we do not consider large MPAs to be the most pragmatic tools for mitigating the effects of climate change, given the extraordinary challenges in implementing and enforcing them and the massive scale of observed and predicted range shifts.

Third, MPA "chains"—networks that are at the scale of or larger than most species range sizes—along a coastline can help mitigate most of the challenges MPAs will face from shifting ranges of species. These stepping stone chains can act like terrestrial migration corridors, which have been recently proposed to protect terrestrial biota with poleward-shifting ranges.[72–74] Individual MPAs in these networks could be relatively small, as their purpose would be to serve as a stepping-stone for shifting species; and the spacing between these MPAs could be determined using biogeographically informed connectivity models (mentioned earlier) to ensure that important species can disperse between them.[75] However, the extent of such an

Table 1. Unique marine features recommended for protection.

Feature to protect	Justification	Example(s)	References
Migration corridors	Terrestrial conservation planning has combined climate velocity models with habitat and species distribution data to identify corridors through which species may shift, which should also be conservation priorities in the ocean.	The southern Appalachian Mountains, which may have served as thermal refugia in the past, are predicted to facilitate the climate-related range shift of many southeast U.S. terrestrial animals.	Lawler *et al.*,[72] McGuire *et al.*[73]
Biogeographic boundaries that lie in path of climate velocity	Coastal marine species that rely on larval dispersal for colonization often cannot cross major breaks in ocean currents. These species may pile up against a poleward biogeographic boundary if they experience mortality at the equatorward edge.	Despite experiencing substantial warming since earliest records, few intertidal species on the east coast of Australia have shifted markedly poleward. A marine biogeographic boundary in the region may be impeding larval dispersal in the direction predicted by climate velocity.	Gaylord and Gaines,[65] Gaines *et al.*,[41] Poloczanska *et al.*,[93] Sorte[66]
Poleward habitat edges	Similar to above, species may pile up at the edge of a habitat that is more climatically suitable than the rest of their historic ranges.	Australian macroalgae in the Indian and Pacific Oceans have retreated from their historic equatorward edge, but cannot colonize poleward past the edge of the continental shelf. Similarly, the ability of North Sea demersal fish to track climate velocity may be constrained by the availability (beyond their historic ranges) of suitable habitat at their preferred depths.	Wernberg *et al.*,[84] Rutterford *et al.*[94]
Thermal refugia/ microrefugia (sites with minimal climate velocity or observed climate change) and climate sinks (sites where many climate velocity trajectories converge, representing locally "lost" climates)	Global climate models predict heterogeneous ocean warming, including thermal refugia and climate sinks that are predicted to accumulate species because they have warmed less than the surrounding environment.	Marine climate sinks may arise when equatorward coastlines block climate velocity trajectories, such as in southern France. Although many parts of the global oceans are not experiencing rapid warming, regional studies (e.g., Brazil and British Columbia) found only a tiny percentage of spatial cells studied that have not and will not experience changing climate conditions.	Dobrowski,[95] Burrows *et al.*,[85] Magris *et al.*,[96] Ban *et al.*[86]
High genetic diversity populations	Some semi-isolated populations are genetically distinct and contribute to high beta-diversity that can increase a species' adaptive capacity. This is sometimes true of equatorward populations of terrestrial and shallow coastal species, which may represent genetically differentiated survivors of past glacial maxima.	The southern range edge of *Bifurcaria bifurcata*, an eastern Atlantic macroalgal species, harbors most of the species' genetic diversity; an ecological niche model for this species predicts loss of the southern population under high (but not low) emissions scenarios. Populations of *Macoma balthica*, a common intertidal bivalve in Europe, exhibit high genetic diversity at the southern range limit—where the range has also contracted due to warming.	Arenas *et al.*,[79] Becquet *et al.*,[97] Neiva *et al.*[98]

NOTE: These unique features in the oceans will (presently or in the future) have disproportionately high conservation value to species experiencing climate change. Most of these features are predicted to aggregate populations and thus become hotspots of species richness.
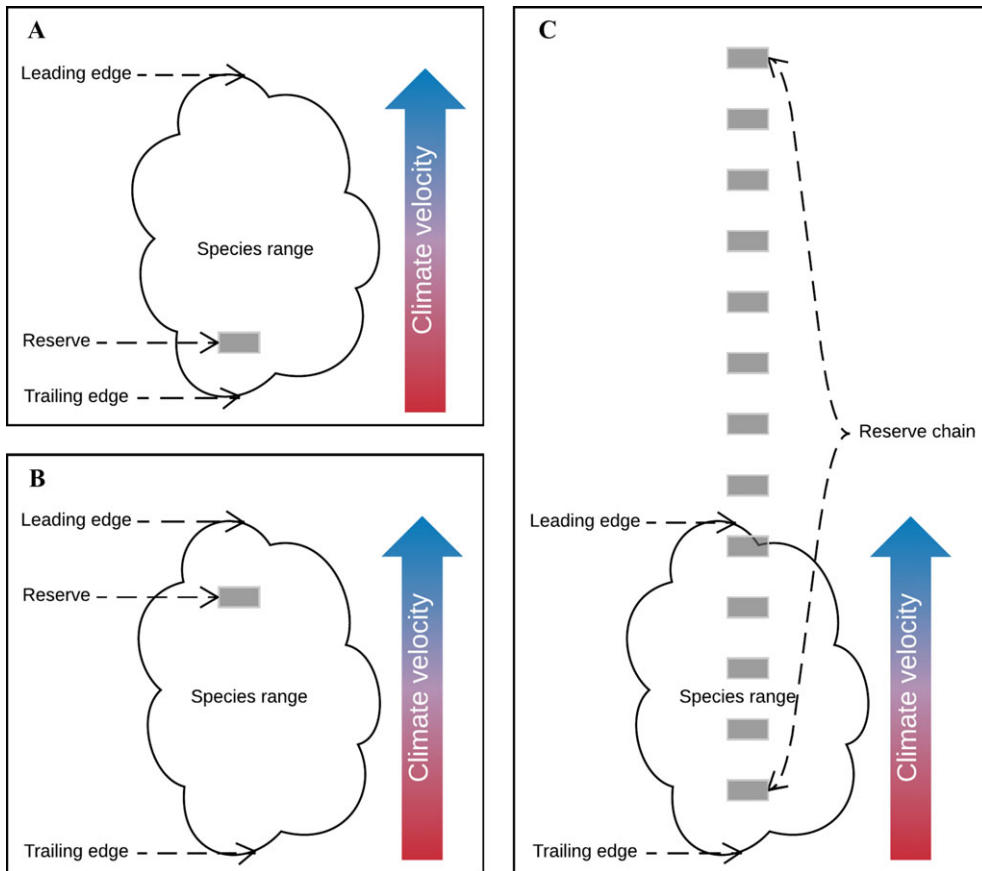
Figure 2. Schematic of MPA configurations in relation to the size of a species' geographic range and the direction of climate velocity. MPAs are positioned near the trailing edge of the species range (A), the leading edge of the range (B), and in a linear chain parallel to climate velocity (C).

MPA chain should encompass a substantial portion of the geographic range of the species or assemblage of interest, in addition to a more distal area that the species or assemblage might shift into (the location and extent of which would be dictated by climate velocity projections) (Fig. 2C). Although an ideal scenario would involve the instantaneous creation of these MPA networks following a unified conservation plan informed by the biogeographic principles described here, we note that MPA chains that emerge from *ad hoc* or sequential planning processes are still likely to confer conservation benefits.[76] However, in scenarios with high uncertainty and/or limited funding, it may be advantageous to strategically postpone conservation interventions to ensure an optimal outcome.[77]

This proposition builds upon, and far exceeds, past calls for MPA networks of up to several hundred

kilometers.[9,57,78] For example, for a species whose range extends 1000 km from north to south, in a region where climate velocity has been estimated at 50 km/decade, an ideal MPA chain intended to protect the species for a century would have to extend most of the species' current range plus an additional 500 km along the path of climate velocity. Although most range-shifting marine species are moving poleward,[67] more refined climate velocity projections for marine assemblages are now available for the global oceans and can be used to inform the orientation of MPA chains.[24] Climate projections have already been used to anticipate climate velocity in North American terrestrial protected areas.[74]

An MPA-chain strategy may be effective at protecting species that are shifting their ranges. However, species cannot shift their ranges indefinitely,

and indeed some are tracking climate velocity slowly or not at all.[25] Thus, our fourth recommendation is to protect areas with high conservation value to species experiencing climate change, such as regions that harbor genetically diverse populations, or areas where species may pass through or aggregate (Table 1). This approach builds upon existing recommendations to protect unique biophysical features in the oceans, such as seamounts, using MPAs.[27,29] The broader conservation literature has also recommended the protection of populations that contribute to genetic diversity, which is generally predicted to be reduced by climate change,[79,80] and the protection of corridors through which wildlife may migrate in response to climate change.[72,73]

We propose additional features for protection with MPAs that, for biogeographic reasons, may aggregate individuals and species in the future and become hotspots of species richness (Table 1). These include biogeographic boundaries that arise from currents, particularly those that account for poleward range edges and may inhibit further range shifts.[65] Marine biogeographic boundaries are often porous and asymmetrical, so knowledge of regional dispersal dynamics and the ability of species with certain life history traits to colonize across specific boundaries will be critical.[41,66,81] These features are somewhat analogous to alpine regions where terrestrial species' trailing edges are shifting upslope, but their leading edges cannot extend further, leading to an overall reduction in habitat and often a concomitant population decline.[82,83] Similarly, because species cannot spread beyond their required habitats, the poleward edges of key marine habitats are likely to play disproportionately large conservation roles.[84] Due to the heterogeneous nature of climate change, some parts of the ocean are predicted to warm much faster than others, and thermal refugia—patches with climatic conditions that have not and are not predicted to change dramatically—could also accumulate species and warrant additional protection,[85] although those refugia may be rare in the oceans.[86] The paths taken by species shifting in response to climate change, termed "migration corridors" in terrestrial ecology, are also likely to accumulate species in the future and contribute substantially to conservation outcomes.[72,73] This concept is most relevant to the coastal oceans, where narrow bands of habitat (possibly along climate

velocity trajectories and/or MPA chains) may serve as a conduit for many species shifting their ranges in the future.

Recognizing that most MPA planning is conducted with spatial prioritization tools that are designed for flexible applications, we stress that all of these considerations can be incorporated into Marxan, Zonation, and other software.[31] For example, poleward range edges may be classified as distinct features with their own representation targets, and the arrangement of MPA chains may be optimized with these tools using projected future species distributions as inputs. In particular, all of the features noted in Table 1 can be easily classified as high-value areas for conservation with these spatial prioritization tools.

Managed relocation (also termed assisted migration or colonization) is a promising but controversial management strategy to conserve species that are declining in their historic ranges. The ecological, ethical, legal, and other challenges facing this intervention have been reviewed elsewhere.[87] Managed relocation has typically been considered an intervention that applies to species that disperse slowly relative to climate velocity, or that have limited habitat availability, such as endemic species with small ranges;[88] it has been most extensively studied in the terrestrial environment, particularly for plants.[89]

From a biogeographic perspective, we note that species' ranges and dispersal patterns will influence both the need for, and the success of, managed relocation. Species with smaller geographic ranges are often more vulnerable to extinction and may need additional conservation efforts.[90] However, the success of those conservation efforts for marine species may hinge on dispersal patterns. As discussed above, biogeography can help to identify regions where marine species may get "stuck" at a dispersal barrier, providing an early flag for species that may need managed relocation. Indeed, managed relocation may be an ideal tool for helping range-shifting species to cross biogeographic boundaries. The same biogeographic principles may also be applied to identify potential habitats for relocation with suitable flow fields that favor self-recruitment.

Conclusions

Many present elements of MPA planning and design have been derived from biogeography, though often

without recognizing that legacy. However, some concepts from biogeography have still not been incorporated into MPA models and theory, particularly regarding the spatial dynamics of marine populations. Biogeographic principles suggest concrete and novel recommendations for MPA design, including the protection of areas that are predicted to aggregate species in this century, and the establishment of massive MPA networks at scales comparable to the geographic ranges of species of interest. These recommendations build upon past calls for larger MPAs and MPA networks. Several relevant topics merit continued research efforts in order to improve MPA design, including the within-range spatial dynamics of marine species, the role of flow fields in structuring dispersal, and the improvement of range shift predictions. By highlighting lessons learned and opportunities to apply them in the climate change context, we hope to improve the design of future MPAs.

Acknowledgments

Supporting Information

Additional supporting information may be found in the online version of this article.

Supplementary File. Code used to produce Figure 1 and calculate statistics in the manuscript. It is provided in a .R file that requires R software (https://www.rproject.org) to open. The file does not include raw data, although the World Database on Protected Areas data can be downloaded online (https://www.protectedplanet.net). The climate velocity and Aquamaps data used in this manuscript are not public.

Competing interests

The authors have no competing interests.

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