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RESEARCH REVIEW

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Incorporating climate change adaptation into marine protected area planning

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Abstract

Climate change is increasingly impacting marine protected areas (MPAs) and MPA networks, yet adaptation strategies are rarely incorporated into MPA design and management plans according to the primary scientific literature. Here we review the state of knowledge for adapting existing and future MPAs to climate change and synthesize case studies (*n* = 27) of how marine conservation planning can respond to shifting environmental conditions. First, we derive a generalized conservation planning framework based on five published frameworks that incorporate climate change adaptation to inform MPA design. We then summarize examples from the scientific literature to assess how conservation goals were defined, vulnerability assessments performed and adaptation strategies incorporated into the design and management of existing or new MPAs. Our analysis revealed that 82% of real-world examples of climate change adaptation in MPA planning derive from tropical reefs, highlighting the need for research in other ecosystems and habitat types. We found contrasting recommendations for adaptation strategies at the planning stage, either focusing only on climate refugia, or aiming for representative protection of areas encompassing the full range of expected climate change impacts. Recommendations for MPA management were more unified and focused on adaptative management approaches. Lastly, we evaluate common barriers to adopting climate change adaptation strategies based on reviewing studies which conducted interviews with MPA managers and other conservation practitioners. This highlights a lack of scientific studies evaluating different adaptation strategies and shortcomings in current governance structures as two major barriers, and we discuss how these could be overcome. Our review provides a comprehensive synthesis of planning frameworks, case studies, adaptation strategies and management actions which can inform a more coordinated global effort to adapt existing and future MPA networks to continued climate change.

KEYWORDS
adaptive management, biodiversity protection, climate change, connectivity, marine protected area network, marine reserve, systematic conservation planning, vulnerability

1 | INTRODUCTION

Marine protected areas (MPAs) and MPA networks are rapidly growing cornerstones of marine conservation efforts worldwide (UNEP-WCMC, IUCN, & NGS, 2018). MPAs can help to increase local biodiversity, restore functional food webs, protect threatened species and sensitive habitats and support adjacent fisheries among other benefits (McCook et al., 2010). Originally, MPAs were designed to protect marine biodiversity from the impacts of overfishing and other human impacts under the implicit assumption of stationary environmental conditions characterized by a mean state with variance, but no long-term trend. Yet, anthropogenic climate change has invalidated that assumption causing rapid and unprecedented shifts in environmental conditions across all ocean basins (IPCC, 2019; Lotze et al., 2019). Marine communities have responded in a multitude of ways including range shifts to higher latitudes or greater depths, altered phenology, and species turnover, among many others (Poloczanska et al., 2016; Worm & Lotze, 2016).

The global MPA network has rapidly expanded over the past two decades as nations work towards meeting the Convention on Biological Diversity's Aichi Target 11 to protect at least 10% of their coastal and marine areas by 2020 (Lubchenco & Grorud-Colvert, 2015). This is particularly relevant in the face of changing ocean conditions as there is evidence that MPAs can help buffer marine communities against the impacts of climate change (Roberts et al., 2017). For instance, benthic invertebrates in an MPA in Mexico had greater resilience to a climate-driven hypoxia event than populations outside of the MPA (Micheli et al., 2012). However, MPAs do not always increase ecosystem resistance to climate-driven events. For example, a global analysis of temperature-driven loss in coral cover found that observed impacts were comparable between protected and unprotected areas (Selig, Casey, & Bruno, 2012). Hence, dramatic reductions in greenhouse gas emissions may be the only comprehensive solution to mitigate the effects of climate change on marine ecosystems (Bates et al., 2019). Regardless, climate change will continue to impact the global network of MPAs (Bruno et al., 2018), posing a significant challenge to managers as to how best to protect marine biodiversity in a changing seascape. To maximize the conservation benefits of MPAs now and into the future climate-change adaptation strategies are critical (Roberts et al., 2017). Yet so far, climate change adaptation is largely limited to conceptual frameworks, and rarely considered in protected areas objectives and management plans (IPBES, 2019; Tittensor et al., 2019).

Here we review the current state of scientific knowledge for adapting MPAs to ongoing climate change. For this review, ‘MPA’ can refer to a single MPA, an MPA network and partially protected MPAs (including ‘other effective area-based conservation measures’; OECMs) or fully protected marine reserves. We started with existing reviews and then performed an extensive search of the primary literature accessible via Google Scholar to answer the question of how marine conservation can best adapt to shifting environmental conditions in a changing climate. Specifically, we introduce conservation planning frameworks that incorporate climate change adaptation into the design and management of MPAs. We derive a simplified generalized planning framework as a guide and then examine how climate change adaptation has been included in MPA planning, design and management with empirical case studies. This includes a discussion of conservation goals, vulnerability assessments, climate change adaptation strategies and management actions in the context of the broader climate change adaptation literature. We further discuss the perceived barriers to including climate change adaptation into MPA design and management, and end on a discussion of research gaps. By summarizing the planning frameworks, case studies, adaptation strategies and management actions, our work can help to inform the development of climate-adaptive MPAs globally.

2 | CONSERVATION PLANNING FRAMEWORKS THAT INCLUDE CLIMATE CHANGE ADAPTATION

Planning frameworks for biodiversity conservation can be used to help design and manage MPAs. A number of frameworks have been proposed which incorporate climate change adaptation (Abrahms, DiPietro, Graffis, & Hollander, 2017; Gross, Woodley, Welling, & Watson, 2016; Poiani, Goldman, Hobson, Hoekstra, & Nelson, 2011; Reside, Butt, & Adams, 2018; Wyborn, van Kerkhoff, Dunlop, Dudley, & Guevara, 2016). These include systematic conservation planning (SCP; Mačić et al., 2018; Margules & Pressey, 2000; Reside et al., 2018), climate-smart conservation (CSC; Stein, Glick, Edelson, & Staudg, 2014), adaptation for conservation targets (ACT; Cross et al., 2012), portfolio decision analysis (PDA; Convertino & Valverde, 2013), and the IUCN adaptation cycle (Gross et al., 2016; see Appendix S1 for details).

The most popular of these planning frameworks are SCP and CSC. SCP is widely implemented in the marine literature, although as of 2015 only ~8% of this literature had considered climate change (Álvarez-Romero et al., 2018). SCP is an 11-step process centred around clear objectives to allocate limited conservation resources (Appendix S1). This process readily allows the incorporation of clear climate change adaptations objectives and three recent reviews have examined SCP in the context of climate change (Álvarez-Romero et al., 2018; Mačić et al., 2018; Reside et al., 2018). CSC, ACT and IUCN adaptation cycle are very similar frameworks based on linking specific climate vulnerabilities and adaptation options to the MPA conservation goals with the IUCN adaptation cycle being the most simplified of the three. PDA is the most dissimilar from the other four planning frameworks and it is based on creating a management action portfolio, similar to a financial portfolio, to maximize conservation benefit while minimizing impacts on human uses in the MPA (Convertino & Valverde, 2013). A recent review and comparison between CSC, ACT and PDA is provided in Abrahms et al. (2017).

We used the five individual planning frameworks to collectively guide our understanding of how climate change adaptation has been incorporated into MPA planning (see Appendix S1 for information on how each framework was included in our summary). To incorporate climate change adaptation into conservation planning, there are four principal steps (Figure 1), based on the general features of the five frameworks listed above. All frameworks set clear conservation goals, which includes defining conservation features (what to protect: such as threatened species) and objectives for the MPA (how to protect: such as defining representation and persistence targets across an MPA). These conservation goals then

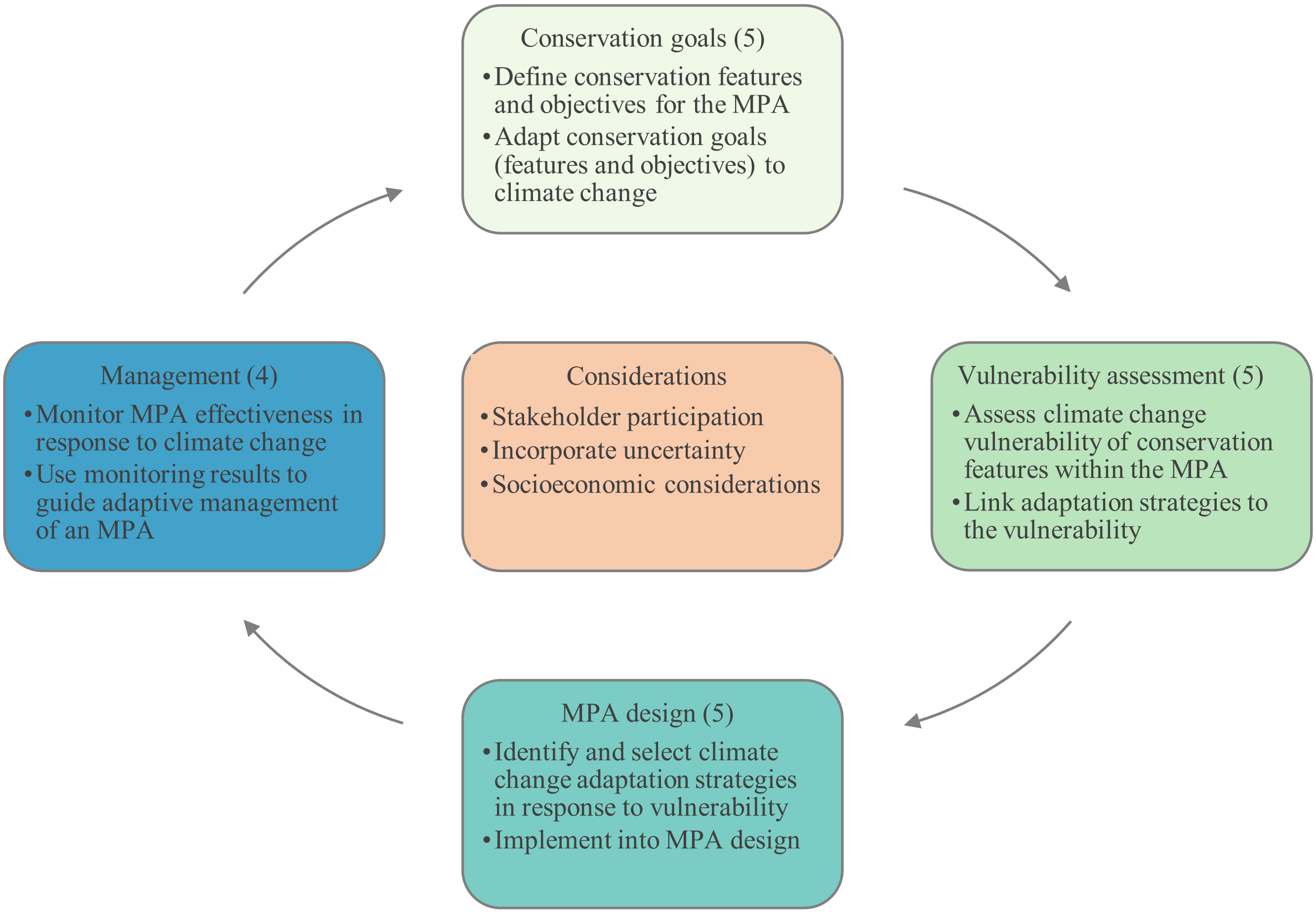


FIGURE 1 Integrating climate change adaptation in all stages of marine protected area (MPA) planning, design and management. Shown is a simplified planning framework based on the general features of five common existing frameworks for biodiversity conservation (see Appendix S1 for details on individual frameworks including how they implemented each measure). Number in brackets indicates number of frameworks (out of five examined) that included these (or equivalent) measures [Colour figure can be viewed at wileyonlinelibrary.com]

need to be adapted to be effective with climate change and may need to be evaluated over time as conservation features may range shift or network connectivity may be disrupted (Carr et al., 2017; Fredston-Hermann, Gaines, & Halpern, 2018). A second step identified by all frameworks is to perform a vulnerability assessment to examine how climate change will impact conservation goals. For example, one conservation feature may be to protect all examples of coral reef bioregions (defined area with unique species assemblages and physical features), with a conservation objective to maintain a certain representation target (e.g. protect 20% of each bioregion). Then a vulnerability assessment may examine how climate change may alter the representation of each bioregion within an MPA (e.g. reductions in spatial coverage results in 10% representation of one bioregion within the MPA) to determine if conservation goals will be met in the future (Game, Watts, Wooldridge, & Possingham, 2008). The third step consists of identifying and selecting climate change adaptation strategies to mitigate against the climate change impacts identified in the vulnerability assessment. These are then incorporated into MPA design, for example by focusing protection on reef features in climate refugia that are projected to experience little or no change in the near future. Finally, as a fourth general step, the MPA would be continually monitored for effectiveness to ensure the conservation goals are being met. The monitoring results can then be used to guide the adaptive management of the MPA against ongoing climate change impacts. Throughout the planning process (Figure 1), it is generally important to (a) include stakeholder participation (Álvarez-Romero et al., 2018); (b) assess the socio-economic impacts of protection (Mangubhai, Wilson, Rumetna, Maturbongs, & Purwanto, 2015); and (c) account for uncertainty in climate change projections, ecological responses and management effectiveness (Hannah, Midgley, & Millar, 2002; Kujala, Moilanen, Araújo, & Cabeza, 2013). This entire planning process may need to be repeated and adapted over time, depending on the results of vulnerability assessments and monitoring data. Although the outlined planning frameworks are generally seen as top–down approaches, bottom-up community efforts can also incorporate climate change adaptation. For example, a locally managed MPA network in Fiji has used adaptive management, in partnership with an NGO, to iteratively refine individual MPA boundaries with coral reef boundaries to enact MPA design principles which may increase resilience to climate change (Weeks & Jupiter, 2013).

3 | HOW CLIMATE CHANGE ADAPTATION CAN BE INCLUDED IN MPA PLANNING, DESIGN AND MANAGEMENT

3.1 | Conservation goals: Define and adapt to climate change

As species and ecosystems continue to respond to a changing climate, MPA conservation goals will need to be re-evaluated and adapted over time (Figure 1; Hopkins, Bailey, & Potts, 2016a). To preserve marine biodiversity in a warming ocean, it is important to include conservation features which focus both on conserving species (fine-filter approaches), while also protecting higher level ecological or environmental aggregations, such as a habitats, eco/bioregions or community/species assemblages (coarse-filter approaches; Tingley, Darling, & Wilcove, 2014). As some species, including threatened, or commercially important species, may be missed when only looking at higher level aggregations, it is important to include both (Tingley et al., 2014). For studies which incorporated climate change adaptation into MPA design, 15% used only species-based (fine-filter) approaches (Figure 2a; Appendix S2), with the rest relatively evenly split between only focusing on higher level aggregations (coarse-filter; 37%) or a mix of the two (both; 48%).

When higher level aggregations were prioritized for conservation, the most common focused on habitat type (e.g. Klein et al., 2013; Maina et al., 2015), followed by eco/bioregions (e.g. Levy & Ban, 2013; Makino et al., 2014), and communities/species assemblages (e.g. Malcolm & Ferrari, 2019; Appendix S2). These approaches were originally designed to protect specific biological communities (Tingley et al., 2014). For instance, Malcolm and Ferrari (2019) used fish assemblage patterns to define a habitat classification system to use in MPA planning within an ocean warming hotspot. They found that despite some tropicalization (increase in proportion of warm water species), the general assemblage patterns persisted over 16 years within the MPA, suggesting that the habitat classification scheme remained a valuable tool. Yet studies like these are likely to remain the exception; species react to a changing climate differently, and re-organizations of biological community structure are likely (Rilov et al., 2019). As such, focus has shifted somewhat from community-centred approaches, such as bioregions, to focus on environmental characteristics or more permanent seascape features, such as habitat type (Tingley et al., 2014).

Habitat type can focus on habitat-forming species, such as corals, oysters or macrophytes, which can provide ecological services to increase community resilience (Simard, Laffoley, & Baxter, 2016), and were included in several design studies (Appendix S2). Some habitat-forming species, such as mangroves and seagrasses, have the added benefit of acting as carbon sinks (Brock, Kenchington, & Martínez-Arroyo, 2012). Yet these habitat-forming species may undergo range shifts requiring a reanalysis of conservation goals. Habitat type can also refer to unusual geological features with complex structure (Stratoudakis et al., 2019), which are permanent even under climate change. Examples include efforts to protect seamounts and underwater canyons (Green et al., 2009; Perdanahardja & Lionata, 2017). Lastly, environmental or climatic conditions can be used to define areas to protect. Typically areas of climate refugia,

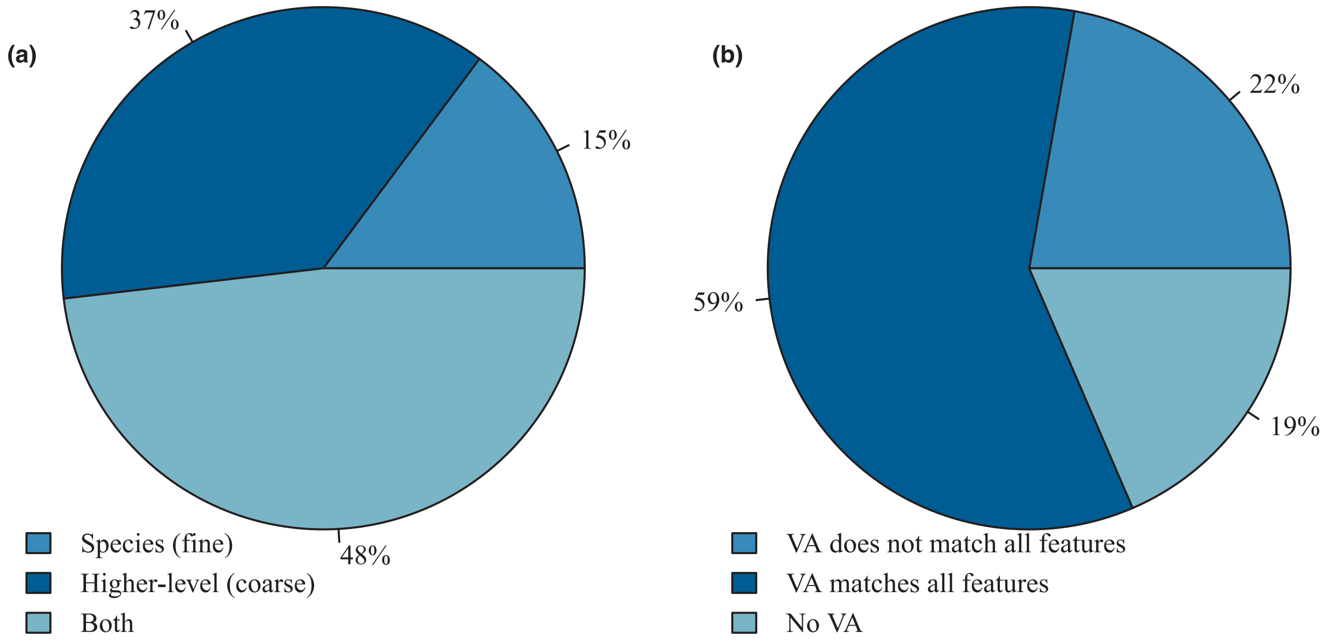


FIGURE 2 Overview of empirical case studies that considered climate change adaptation in the design of existing or future marine protected areas (MPAs; *n* = 27). (a) Conservation features prioritized for protection within the MPA, including species-based (fine), higher-level environmental or biological aggregations (coarse), or a combination of the two (both). (b) If a climate change vulnerability assessment (VA) was performed as part of the MPA planning process and if it matches all or not all conservation features. For further details see Appendix S2 [Colour figure can be viewed at wileyonlinelibrary.com]

where conditions are not changing or changing only slowly, have been prioritized for protection (Fredston-Hermann et al., 2018; Tingley et al., 2014). Others argue, however, that areas including the full range of projected climate change impacts should be considered to ensure the protection of the full spectrum of 'climate heterogeneity', in other words include areas projected to have different exposure to climate change (Gerber, Mancha-Cisneros, O'Connor, & Selig, 2014). Simulations of coral reef ecosystems have shown that as corals adapt to changing conditions, habitat diversity is the preferred adaptation strategy over climate refugia (Walsworth et al., 2019).

By protecting habitats experiencing the full range of climate projections, MPAs are best facilitating the ability of different species to adapt and evolve, or shift their distribution, particularly if connectivity is maintained between MPAs (Brock et al., 2012; Webster et al., 2017). For instance, Magris, Pressey, Mills, Vila-Nova, and Floeter (2017) prioritized a combination of refugia coral reefs and reefs exposed to warming temperatures for protection, while facilitating connectivity via source reefs (that export larvae to nearby habitats) and stepping stones (small habitat patches that species colonize to facilitate longer distance dispersal). Furthermore, if functional groups are protected across the full range of environmental conditions, ecosystem functions can be maintained as each trophic level has a role in regulating an ecosystem (McLeod, Salm, Green, & Almany, 2009; Simard et al., 2016). This has been incorporated into MPA conservation features by conserving herbivorous fish to increase coral reef resilience to climate change (Mumby, Wolff, Bozec, Chollett, & Halloran, 2014; Weeks & Jupiter, 2013). Protecting areas of high species diversity, genetic diversity and critical habitat areas have also been suggested as an important climate change conservation strategies (Brock et al., 2012; Fredston-Hermann et al., 2018), and were included in several design studies (Appendix S2).

Protecting species with crucial ecosystem roles, or of ecological concern, is an important biodiversity conservation goal in the face of climate change (Brock et al., 2012). When climate change was incorporated into MPA design with only species-based approaches (Appendix S2) these studies generally focused on protecting keystone species (Patrizzi & Dobrovolski, 2018) or used species-specific trait-based vulnerability to warming, such as coral reef thermal stress regimes (Magris, Heron, & Pressey, 2015; Mumby et al., 2011). The thermal stress regimes each denote different levels of projected coral stress, across various magnitudes of climate change exposure, to define a range of areas to protect across different climate futures. In mixed approaches (Appendix S2), individual species were included if they were threatened, endemic commercially or ecologically important, or were associated with a specific habitat area (e.g. Green et al., 2009; Lombard et al., 2007; Magris et al., 2017). Regardless of the type of conservation feature that was protected, similar conservation objectives were used in all case studies. All considered some type of climate change objective, also known as persistence targets, to ensure a conservation feature persists in the face of climate change (Appendix S2). Most (86%) of studies defined representation targets to be met within the MPA (e.g. 30% of the total habitat extent of a specific habitat). Many (63%) included socio-economic consideration such as minimizing loss to fishers, and some included objectives to maintain connectivity within an MPA network (26%).

3.2 | Vulnerability assessment: Testing for climate change vulnerability

Before climate change adaptation strategies can be incorporated into MPA design and management, the specific vulnerability of the conservation features to climate change must be assessed (Figure 1; Foden et al., 2019). Climate change vulnerability has three components: exposure, sensitivity and adaptive capacity (Dawson, Jackson, House, Prentice, & Mace, 2011). Exposure quantifies the amount of climate change expected to impact the conservation feature, for example, the rate and magnitude of sea surface temperature (SST) increases. Sensitivity is the dependence of a conservation feature on a given set of abiotic or biotic conditions, for example, some species can tolerate greater SST increases. Adaptive capacity is the ability of the conservation feature to deal with climate change through mechanisms such as phenotypic plasticity, evolutionary processes or range shifts. Climate change vulnerability has been examined in existing MPAs where it can inform management actions such as rezoning (Keller et al., 2009). It can also be included within the design phase of MPA planning during spatial prioritization to allow for the implementation of climate change adaptation techniques (Jones, Watson, Possingham, & Klein, 2016).

We examined how the vulnerability of MPAs to climate change has been assessed in the design phase of MPA planning (Figure 3; Appendix S2). Here we only focus on biological and not on the socio-economic response to climate change, but note that both be incorporated into the vulnerability assessment (Figure 1; Maxwell, Venter, Jones, & Watson, 2015). We found that 81% of case studies included a vulnerability assessment (Figure 2b). These were performed almost exclusively on corals (82%; Figure 3c). This meant that for almost a quarter of the case studies, not all conservation features within an MPA underwent a vulnerability assessment (Figure 2b). For instance, Magris et al. (2017) used thermal stress regimes for corals as a vulnerability assessment to prioritize refugia and disturbed reefs for protection. Coral reefs provide important biogenic habitat and can be considered a sentinel species, indicating broader changes in an MPA. Yet, no vulnerability assessment was performed for other conservation features such as threatened or endemic species. Different temperature tolerances between species and within a taxon (e.g., between coral species; Gibbin, Putnam, Gates, Nitschke, & Davy, 2015) result in species-specific climate vulnerability, and the inclusion of impacts across an entire ecosystem may suggest different areas to prioritize for protection (Rilov et al., 2019). Yet only a few studies exist on how to examine ecosystem wide climate change vulnerability within existing MPAs (e.g. Kay & Butenschön, 2018; Munguia-Vega et al., 2018; Queirós et al., 2016). For instance, Munguia-Vega et al. (2018) used a literature review to qualitatively synthesize ecosystem level climate change vulnerability across multiple studies for an MPA network in

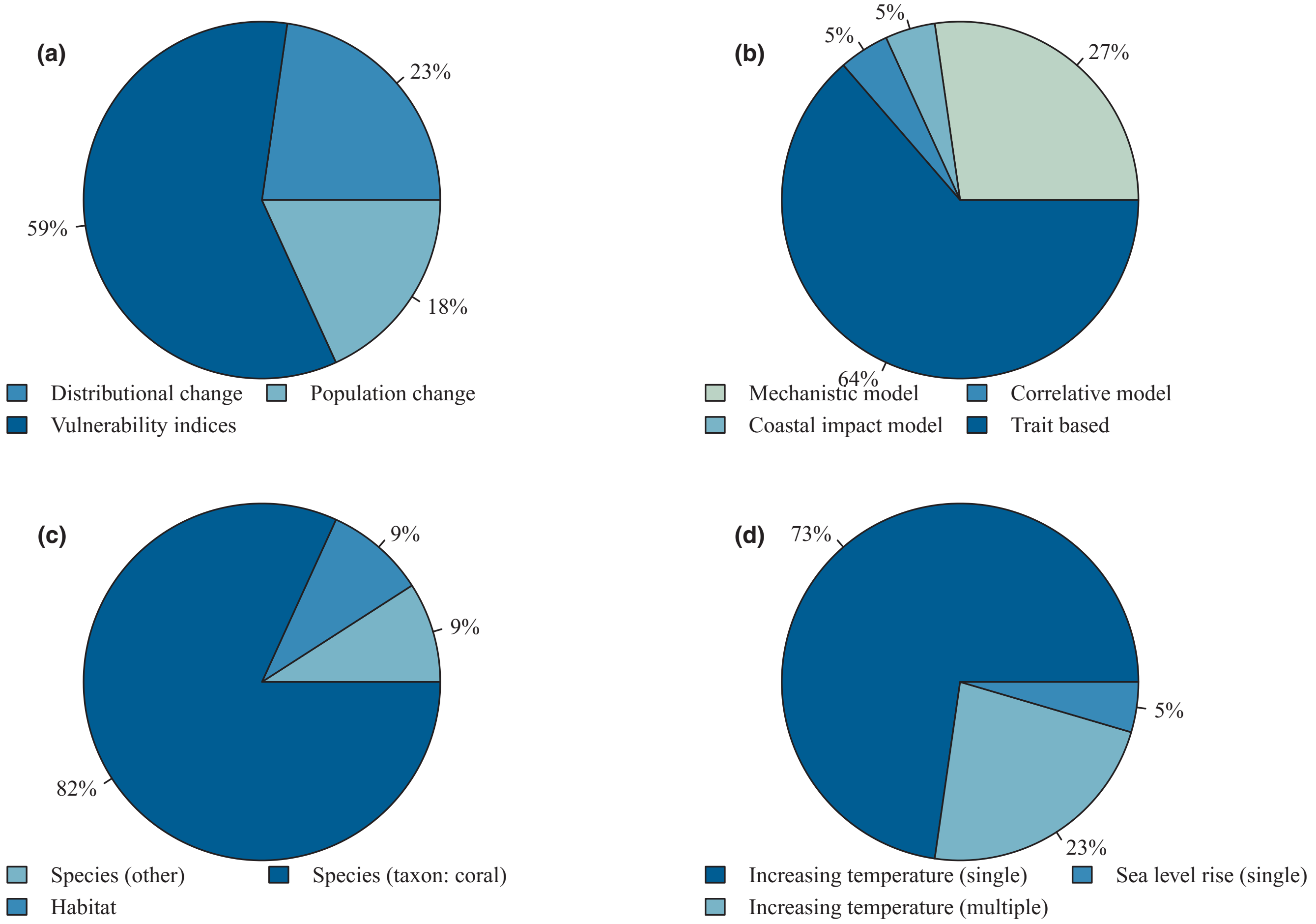


FIGURE 3 Empirical case studies that included a vulnerability assessment during the design of existing or future marine protected areas (*n* = 22). (a) The metric of how climate change will impact the conservation feature. (b) What type of model was used to assess the vulnerability. (c) What ecological resolution was used to examine the vulnerability. (d) What climate change threats were included in the assessment, and if the threat was examined in isolation (single) or in conjunction with other climate change stressors (multiple). For further details see Appendix S2 [Colour figure can be viewed at wileyonlinelibrary.com]

the Gulf of California. No case studies incorporated ecosystem wide climate change vulnerability into MPA design (Appendix S2).

Four main approaches have been used to assess a species' vulnerability to climate change: correlative, mechanistic, trait-based and combined approaches (Figure 3b) to model range shifts, extinction probability, population changes, and to create vulnerability indices (Figure 3a; Foden et al., 2019; Pacifici et al., 2015). Correlative and mechanistic models generally test for climate change exposure, while trait-based approaches test for sensitivity and adaptive capacity (Willis et al., 2015). Trait-based assessments have been widely used as many species can be assessed at once (Foden et al., 2019). We found that trait-based approaches were the most common method used to assess vulnerability in MPAs (Figure 3b), particularly those based on thermal stress regimes to identify coral bleaching risk. Thermal stress regimes use observed and sometimes future projected SST data to calculate metrics of acute (e.g. degree heating weeks) and chronic (e.g. rate of SST warming) stress to determine potential climate refugia (low exposure to thermal stress) and areas where corals may have high adaptive capacity due to previous or projected exposure to thermal stress (Chollett, Enríquez, & Mumby, 2014; Magris et al., 2015). Other trait-based methods included using susceptibility models to develop an exposure metric (Maina et al., 2015), or using thermal thresholds to examine distributional changes (Makino et al., 2014). Literature reviews and expert knowledge have also been used to qualitatively discuss vulnerability within the MPA or the results from the literature search have been used to make a quantifiable metric of a resilience indicator. For instance, Davies et al. (2016) used a literature review to identify the traits that may increase coral resilience to develop six, ranked resilience indicators that were included in MPA design.

With more knowledge, a species distribution model (SDM) can be used to explicitly test for future changes in habitat suitability (Foden et al., 2019). While SDMs were the most commonly used tool to incorporate climate change in a global review of spatial prioritization techniques (Jones et al., 2016) we found that only one study (Patrizzi & Dobrovolski, 2018) used SDMs to test for species distribution shifts with climate change within the context of MPA design (Figure 3a,b; Appendix S2). This study built SDMs for 17 threatened starfish species and their predicted current and future distributions were used to spatially prioritize areas for protection (Patrizzi & Dobrovolski, 2018). Other studies have used SDMs to examine climate change vulnerability within existing MPAs and their management (e.g., Jones et al., 2013). Yet the scarcity of SDMs used in designing MPAs is likely due to terrestrial bias in the global study (76%; Jones et al., 2016) and the greater use of SDMs in terrestrial compared to marine environments (Robinson et al., 2011). The most data-intensive and robust vulnerability approach uses process-based mechanistic models (Foden et al., 2019). We found that 27% of studies used mechanistic models to test for changes in coral per cent cover (Beger et al., 2015) and shifts in fish and invertebrate larval distribution (Álvarez-Romero et al., 2018).

In terms of climate change threats considered in the vulnerability assessments, we found that increasing temperature was by far the most common one (Figure 3d). Increasing temperatures were either examined in isolation (73% of studies) or in interaction with other climate-induced threats (23%). These interactions were most often examined with ocean acidification, changes in primary productivity or changes in UV radiation (Appendix S2). The interaction of multiple climate change stressors is important to include in vulnerability assessments, as predictions based on one stressor can be misleading (Worm & Lotze, 2016). Which threats to examine will be specific to the conservation goals of an MPA (Figure 1). For example, in tropical environments, increasing temperatures, rising sea level and decreasing pH will have negative impacts on coral reefs (McLeod et al., 2012). About 19% of the studies did not specify a specific climate change threat, and instead considered climate change adaptation in MPA design according to general resilience principles (Figure 2a).

3.3 | MPA design: Identify, select and implement climate change adaptation strategies

After a vulnerability assessment has been performed, specific adaptation strategies can be used in MPA design to minimize vulnerabilities (Figure 1). We reviewed the literature to extract climate change adaptation strategies that have been incorporated into MPA design (Figure 4; Appendix S2). Ideally, climate change considerations should be included early in the design process (Hopkins et al., 2016a). Furthermore, as there is often considerable uncertainty associated with climate change, conservation goals, adaptation strategies and management options must be robust or adaptable to different scenarios (Hopkins et al., 2016a) and include margins of error (Baron et al., 2009; McCook et al., 2009). The following sections define different adaptation strategies, explain how they were incorporated into MPA design and explore how they fit into the broader conservation literature.

3.3.1 | Increase MPA resilience

The earliest attempts to include climate change adaptation into MPA design were based on general guidelines to increase the resilience of coral reefs to climate change (McLeod et al., 2009). Resilience in this context is defined as the ability of an ecosystem to resist, recover or adapt to climate change while maintaining key ecosystem functions and services (Holling, 1973; Nyström & Folke, 2001). We found that 45% of studies used general resilience factors as the climate change adaptation strategy in MPA design (Figure 4). These resilience principles included recommendations on minimum MPA size, MPA shape, how to spread risk with representation and replication targets, how to protect critical habitat areas (ecologically important and climate refugia), maintain connectivity (for larval dispersal, connection of mobile species and interconnectivity of different habitat types), maintain ecosystem function, allow time for recovery, reduce other stressors and use ecosystem-based management (Green et al., 2014; Keller et al., 2009; McCook et al., 2009; McLeod et al., 2009). A recent review found 45 biological and physical attributes that contribute resilience to climate change across different ecological levels of organization (Timpane-Padgham, Beechie, & Klinger, 2017). As such, some studies have identified their own MPA-specific resilience features that are prioritized for protection. For example, representation targets were set in a proposed redesign of the Ningaloo Marine Park in Australia for structural complexity, water mixing, seaweed coverage, coral cover, proximity to human activities and minimum water depth as features that increase resilience to ensure adequate representation of areas that are most resistant or likely to recover from thermal disturbances (Davies et al., 2016).

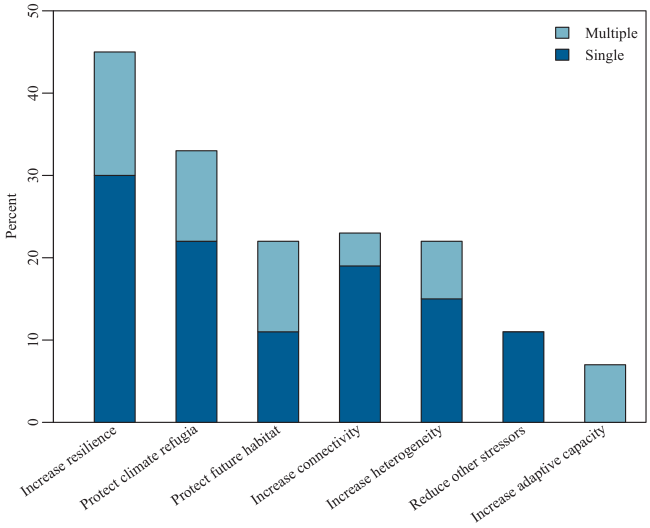


FIGURE 4 Climate change adaptation strategies for marine protected areas (MPAs). Shown are the common strategies employed relative to the total number of studies that considered climate change adaptation in the design of existing or future MPAs (new or redesign of existing; *n* = 27). Strategies were used in isolation (dark shade) or in conjunction with other strategies (light shade). For further details see Appendix S2 [Colour figure can be viewed at wileyonlinelibrary.com]

These resilience principles are grounded in accepted design principles which are often applied outside the context of climate change (Roberts, Halpern, Palumbi, & Warner, 2001). But they have also been used in the design of a few MPA networks to specifically increase climate change resilience; for example in Kimbe Bay, Papua

New Guinea (Green et al., 2009). The design protected each conservation goal with a conservation objective based on three distinct replicates covering 20% of its total distribution (20% representation target). Fish spawning areas and turtle nesting sites were protected as critical habitat, and connectivity of shallow water habitats was incorporated by the automatic clustering of adjacent habitats. Due to data limitations they were unable to include more quantifiable methods of connectivity and used expert knowledge of coral bleaching vulnerability as a proxy for impacts of rising temperatures and coastal slope as a proxy for sea level rise. Similar approaches have been taken for MPA networks in Fiji (Weeks & Jupiter, 2013) and Indonesia (Mangubhai et al., 2015).

3.3.2 | Protect climate refugia

Another common adaptation measure is the protection of climate refugia, here defined as slower changing areas where species, habitats or ecosystems may be more likely to persist (Keppel et al., 2015; Schneider, 2018). Refugia occur from regional to small scales, while microclimates may provide refuges at scales of 10's of metres (Woodson et al., 2019). As there remains uncertainty around the effectiveness of MPAs in increasing ecosystem resilience to climate change, one argument for protecting refugia is that they might provide their full array of ecological benefits to the widest diversity of species as conditions are not changing, instead of only disturbance-tolerant species in a warming MPA (Côté & Darling, 2010). Protecting refugia may also be a way of 'buying time' to allow for species and ecosystems to adapt to changing conditions, despite their limited temporal (Keppel et al., 2015) and spatial (Ban, Alidina, Okey, Gregg, & Ban, 2016) scale of protection. Yet, they should not be the only climate future incorporated into MPA design (Tittensor et al., 2019).

We found that 33% of studies focused on protecting refugia as the key climate change adaptation strategy (Figure 4), for example, by including areas with cold-water upwelling to protect coral reefs from increasing temperatures (Perdanahardja & Lionata, 2017). However, the timing of cold-water upwelling events must also coincide with the timing of thermal stress, which may not always be the case (Chollett, Mumby, & Cortés, 2010). Using information about a range of current climate conditions, more quantifiable susceptibility models, or exposure metrics, can be generated to quantify current exposure to climate stress and prioritize areas with low exposure for protection. These can be based on several environmental data layers (Allnutt et al., 2012; Klein et al., 2013; Maina et al., 2015) or use information from SST only (Ban, Pressey, & Weeks, 2012). A key assumption with this approach is that areas with currently low exposure to thermal stress will continue to have low exposure into the future. To test if this assumption holds true, information about future projected climate conditions can be integrated. For example, coral bleaching risk up to 2100 has been examined based on where SST is projected to increase above a bleaching threshold to prioritize refuge areas for protection where the risk of bleaching was lowest (Game, Watts, et al., 2008; Levy & Ban, 2013). Ideally, future projected conditions are based on regionally downscaled output from earth system models (e.g. van Hooidonk, Maynard, Liu, & Lee, 2015), which alone often offer too coarse a spatial resolution for local management (Kwiatkowski, Halloran, Mumby, & Stephenson, 2014). Alternatively, historical satellite SST data can be used to understand patterns of local temperature variability over time and predict future refugial areas. However, this assumes that spatial patterns of temperature variability will persist into the future (Chollett et al., 2014).

3.3.3 | Protect future habitat

When projections exist for a species or habitat's future distribution, MPAs can be designed to prioritize those areas for protection that will either harbour key species or habitats in the future, or remain suitable for a certain time period (Jones et al., 2016; Soto, 2002). The key difference between protecting climate refugia and future habitat is that the latter can occur in an area with high climate change exposure. We found that 22% of studies prioritized future habitat for protection as the climate change adaptation strategy (Figure 4). For example, Runting, Wilson, and Rhodes (2013) prioritized areas where different wetland habitat types were expected to be found in the future, given projected sea level rise. Yet, many conservation processes require species presence in an MPA now, and not at a theoretical time in the future (Hopkins et al., 2016a). Therefore, most studies that focus on future habitat prioritize habitats that currently exist and are expected to continue to exist into the future. For example, a proposed redesign of an MPA network in Brazil found that if climate continues to warm, the most efficient MPA design would include both current and future distribution of threatened starfish species, based on SDMs (Patrizzi & Dobrovolski, 2018). Other approaches have modelled projected changes in coral cover to ensure it would remain at a suitable level within the MPA network over a specified time (Beger et al., 2015), or have incorporated connectivity metrics to prioritize current and future habitat (Makino et al., 2014, 2015).

3.3.4 | Increase connectivity

Increasing connectivity was the most commonly recommended climate change adaptation strategy for biodiversity management (Heller & Zavaleta, 2009). We found that 23% of studies increased connectivity as their adaptation strategy, tied with protecting future habitat and ~10% less than the protecting refugia (Figure 4). This in part may be due to the higher data requirements needed to accurately model connectivity (Friesen, Martone, Rubidge, Baggio, & Ban, 2019), whereas climate refugia can be categorized with only climate projections. Ensuring connectivity within an MPA network helps facilitate species persistence (McCook et al., 2009), and increases MPA benefits for the marine ecosystem (Carr et al., 2017; Olds et al., 2016). Climate change is expected to change connectivity in many different ways, such as by altering circulation patterns and stratification

(Gerber et al., 2014; Munday et al., 2009). Such changes in connectivity should be directly included in reserve design with ecologically justified statements rather than indirectly addressed through changes in MPA size (generally larger is better) or distance (closer; Magris, Pressey, Weeks, & Ban, 2014). Specific guidelines on how large an MPA should be will vary depending on the conservation goals (Carr et al., 2017). Ideally, both ecological (e.g. dispersal distances) and physical (e.g. currents) linkages would inform dynamic models of species transport and movement across all life stages under different climatic conditions, including source, sink, migration and stepping-stone areas as priorities for protection (Brock et al., 2012; McCook et al., 2009; Salm, Done, & McLeod, 2006). In practice, this is likely only possible for a few well-understood species.

Projected shifts in oceanographic currents for larval transport should be considered in MPA design (Foley et al., 2010) as they can impact dispersal distances, which necessitates MPAs being placed closer together to maintain connectivity (Gerber et al., 2014). To test this, Andrello, Mouillot, Somot, Thuiller, and Manel (2015) used a mechanistic model of larval transport driven by changes in current velocities to show that average larval dispersal distance would decrease in the Mediterranean Sea but connectivity within some MPAs would increase as new areas became suitable habitat. Other climate change impacts will also affect larval connectivity. Using a simulated 3°C increase in ocean temperature, planktonic larval duration was shown to decrease in the Gulf of California. This provided an ecological justification for the idea that larger, closer MPAs are required, instead of following general rules of thumb (Álvarez-Romero et al., 2018). Lastly, connectivity can be maintained by protecting climate (migration) corridors that allow species to track shifts in climate between MPAs (Beier, 2012), particularly if climate corridors follow local climate velocities (Fredston-Hermann et al., 2018). Yet, increasing connectivity can also interfere with adaptation if incoming genetic diversity reduces the prevalence of heat-resistant genotypes within a population (Mumby et al., 2011). In such cases, connectivity should be maintained across populations exposed to similar environmental conditions so as not to reduce genetic drift promoting adaptation to warming temperatures.

3.3.5 | Increase heterogeneity

Building on the protection of climate refugia, increasing heterogeneity aims to protect areas across the full range of climate change impacts including climate refugia, areas with high climate variability and high-exposure areas (Jones et al., 2016). This strategy adds the benefits of protecting climate refugia (discussed above) to those of protecting areas with greater climate variability which can increase the phenotypic plasticity of local populations (Boyd et al., 2016). Additionally, as climate change can drive rapid natural selection within disturbed populations, protecting high-exposure areas can promote local adaptation (Rilov et al., 2019). Furthermore, by protecting both low exposure areas where non-disturbance-tolerant species are afforded protection, and high exposure areas where protection facilitates adaptation with the potential for recovery after climate-driven events, the likelihood that healthy ecosystems can persist is increased (Game, McDonald-Madden, Puotinen, & Possingham, 2008). If connectivity is maintained across the full spectrum of climate heterogeneity, then the MPA network is facilitating adaptation at different spatial, temporal and taxonomic scales, a strategy known as 'adaptation networks' or increasing adaptive capacity (Webster et al., 2017). For example, Mumby et al. (2011) used thermal stress regimes to define hypothesized future coral reef health and linked these with larval dispersal predictions to prioritize reefs for protection that promote high genetic adaptation and phenotypic acclimation potential.

We found that 22% of studies focused on protecting areas across a gradient of climate heterogeneity as the climate change adaptation strategy in MPA design (Figure 4). Generally, different management strategies and representation targets are set across different levels of climate change exposure. Using a conceptual model of low and high climate change exposure, fishing pressure and biodiversity value, Allnutt et al. (2012) assigned different management actions across areas of high and low values of each metric. Magris et al. (2015) defined different representation targets for MPA network design for nine different combinations of exposure to thermal stress. For instance, 100% representation targets were set both for areas with low observed and future rates of exposure, providing thermal refugia now and into the future, and areas with high observed and future exposure, protecting potentially disturbance-tolerant species with high resistance to warming.

3.3.6 | Reduce other stressors

MPA managers can do little to reduce the direct climate change impacts in MPAs (but see Macgregor & van Dijk, 2014; Mawdsley, O'Malley, & Ojima, 2009; West et al., 2009). Yet management actions can be taken to reduce other stressors and minimize cumulative impacts (Gurney, Melbourne-Thomas, Geronimo, Aliño, & Johnson, 2013), thereby increasing the resilience of marine ecosystems to climate change impacts (Mcleod et al., 2019). We found that 11% of studies focused on reducing other stressors as the climate change adaptation strategy in MPA design (Figure 4). To do so, information on different land-based, fishing and climate change stressors can be used to inform habitat condition to prioritize habitats where stress is low and habitat condition is assumed to be high (Klein et al., 2013). Other examples include explicitly linking land-use and climate change scenarios to prioritize protecting land areas upstream from MPAs to reduce the impact of land-based stressors (Delevaux et al., 2018, 2019).

3.3.7 | Other methods

While the above-mentioned adaptation strategies have been incorporated into some MPA designs (Appendix S2), others ideas exist in the literature that have yet to be documented in published applications, least as published in the scientific literature (Heller & Zavaleta, 2009; Rilov et al., 2019). Of particular interest are dynamic MPAs, which can move in space and time. Dynamic MPAs could be used to rotate protection across MPAs in coral reefs to protect herbivorous fish which can increase ecosystem resilience (Game, Bode, McDonald-Madden, Grantham, & Possingham, 2009). Dynamic MPAs could also track changing environmental conditions by tracking shifts of SST fronts which often harbour aggregations of vulnerable marine predators (Hannah, 2008), or move with species as their range shifts in response to climate change (Hobday, 2011). Dynamic MPAs could be used in conjunction with permanent MPAs to create flexible networks which draw on the benefits of permanent and dynamic MPAs (D'Aloia et al., 2019; Tittensor et al., 2019).

3.4 | MPA management: Managing for climate change

Effective management is critical to the success of any MPA, even without the added impacts of climate change (Gill et al., 2017). Ecosystem-based management was initially proposed as a central resilience principle for MPA networks incorporating climate change adaptation (McLeod et al., 2009). A global meta-analysis found that with proper management, partially protected areas promote greater fish abundance and biomass than unprotected areas, and this benefit was enhanced when placed adjacent to a marine reserve (Zupan et al., 2018). As such it has been proposed that MPA networks be built around core no-take marine reserves managed in conjunction with partially protected MPAs or OECMs and managed within a wider seascape in which fisheries and other ocean uses are managed appropriately (e.g. invasive species, pollution; Keller et al., 2009; Wenzel et al., 2016). Recently there has been a shift to resilience-based management, which builds on ecosystem-based management by acknowledging that humans are a driver of change in marine ecosystems, to identify and prioritize management actions to promote ecosystem resilience and facilitate adaptation (reviewed in Mcleod et al., 2019).

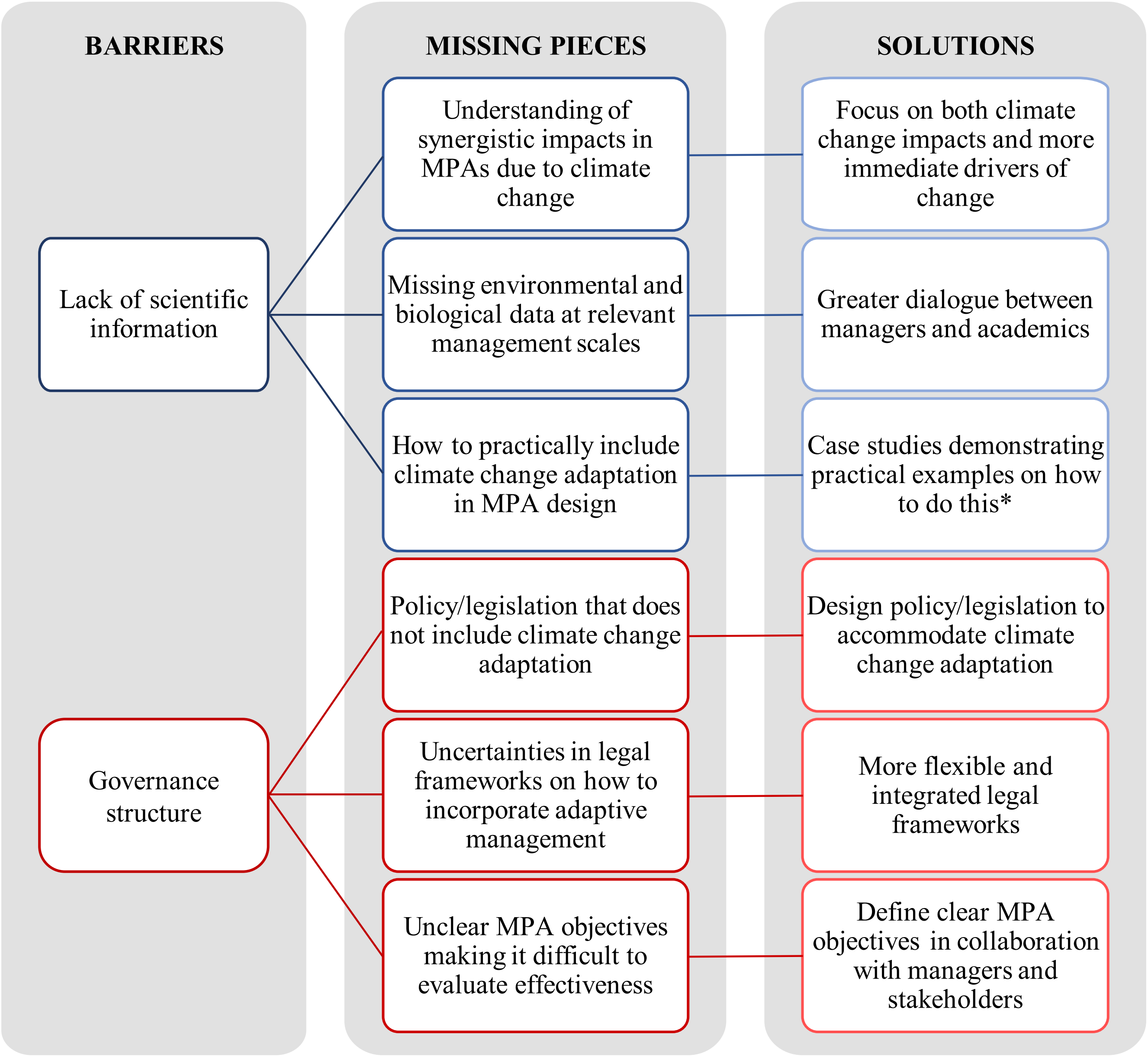
Due to the global scale of climate change, management for climate change impacts should be coordinated across the entire MPA network, with regional management focusing on smaller scale impacts such as land-based pollution (Mach et al., 2017) and transboundary partnerships to facilitate range-shifting species (Hannah, 2010). Management may best build synergies by coordinating centralized governance and local community governance that includes input from a diverse stakeholders with different capacities to promote climate change adaptation (Ma, 2018; Tuda & Machumu, 2019). Climate change should also be incorporated into management plans with varying scenarios accounting for uncertainty (Hannah et al., 2002). Management actions that target mitigation, repair (e.g. assisted evolution) and societal adaptation (e.g. to loss of coastal protection) will also play a role (Comte & Pendleton, 2018; Rogers et al., 2015).

To increase management effectiveness, adaptive management is one of the most widely cited climate change adaptation strategies (Heller & Zavaleta, 2009), and an important component of resilience-based management (Mcleod et al., 2019). We found that only one of the case studies (~4%) had used adaptive management, but as a caveat we did not review all existing MPA management plans; thus, adaptative management may be more prevalent. Adaptive management uses new information to iteratively update management goals and methods either passively from past experiences or actively through experimentation with carefully designed monitoring (Ban et al., 2011). As such adaptive management can be used in MPAs to continually respond to ongoing climate change impacts. This can address uncertainty surrounding climate change impacts in conservation planning, as plans can be continually updated (Ban et al., 2011; Mcleod et al., 2019). Updates to plans can include rezoning (Keller et al., 2009) or re-delineating MPA network boundaries (Weeks & Jupiter, 2013). Adaptive management can help to correct any errors made during the initial planning process (Magris et al., 2014). It can increase the clarity of management actions if a diverse group of stakeholders is included throughout the process to promote support and compliance within an MPA (Mcleod et al., 2019).

In order for adaptive management to be effective, monitoring programmes targeting multiple indicators for ecological and social effectiveness in MPAs are required (Carr et al., 2017; Mcleod et al., 2019). Indicators can be based on climate-driven ecological thresholds that are indicative of phase shifts, providing early warning signs to inform where management intervention should focus (Johnson & Holbrook, 2014). Indicators can also track other climate-driven changes such as species range shifts, alterations in community assemblages groups, reductions in sentinel species coverage (e.g. seagrass) or changes in resilience (Maynard, Marshall, Johnson, & Harman, 2010; Otero, Garrabou, & Vargas, 2013). The chosen indicators will be specific to the geographic region and conservation goals an MPA has (Carr et al., 2017; Mcleod et al., 2019). For instance, if an MPA network goal is to promote connectivity, monitoring could examine the transport of juveniles from nursery areas to other habitats as an indicator of MPA effectiveness (Carr et al., 2017). Monitoring programmes should include targeted (standardized) and surveillance (observational) monitoring over the long term to understand changes in MPA environmental and ecological conditions, as well as short-term studies to understand specific processes within MPAs (Rannow et al., 2014; Salm et al., 2006). To be effective, monitoring programmes need to be designed at the appropriate spatial and temporal scale (Baron et al., 2009; Carr et al., 2017). They should also include human drivers that can affect a species/ecosystems vulnerability within an MPA (Mcleod et al., 2019). For instance, physical barriers to protect against sea level rise can have indirect negative impacts on marine ecosystems ability to migrate and adapt in response to sea level rise and other climate impacts (Maxwell et al., 2015).

4 | BARRIERS TO CLIMATE CHANGE ADAPTATION

Reviewing studies which had conducted interviews with MPA managers and other individuals involved in the planning and implementation process (Cvitanovic, Marshall, Wilson, Dobbs, & Hobday, 2014; Hagerman & Satterfield, 2014; Hopkins et al., 2016a) offers insight into the perceived barriers for embracing climate change adaptation in marine conservation planning (Figure 5). Despite recognizing a need to act with current knowledge, in full awareness of uncertainty (Hagerman & Satterfield, 2014; Simard et al., 2016), a lack of scientific information is often listed as a major barrier to climate change adaptation (Cvitanovic et al., 2014; Hagerman & Satterfield, 2014; Hopkins et al., 2016a). Missing information includes an understanding of synergistic impacts of climate change and other stressors in MPAs. There are concerns that by focusing on climate change adaptation strategies, more immediate drivers of change might be sidelined (Hagerman & Satterfield, 2014). A second limitation is missing environmental and biological climate change impact data at a relevant scale to management as most climate change projections are based on global climate models. There is a recognized need for greater dialogue between academics and policymakers (Petes, Howard, Helmuth, & Fly, 2014). Interestingly, although MPA managers recognize the importance of peer-reviewed science to inform decision-making, it is not always thought to be less biased than other information sources (Cvitanovic et al., 2014), and is sometimes valued and used less than data collected by government staff (Lemieux, Groulx, Bocking, & Beechey, 2018). The third source



*See supplementary information for a list of case studies

FIGURE 5 Barriers to climate change adaptation. Perceived general barriers, specific missing pieces and potential solutions to implementing climate change adaptation in marine protected areas (MPAs) were identified by reviewing interview-based studies with MPA managers and other individuals involved in the MPA planning and implementation process [Colour figure can be viewed at wileyonlinelibrary.com] of limited scientific information is a lack of thorough understanding of how adaptation can be practically incorporated into marine conservation planning and management (Cvitanovic et al., 2014; Hagerman & Satterfield, 2014; Hopkins et al., 2016a). MPA managers value peer-reviewed research based on case studies that provide relevant and realistic examples of how climate change adaptation can be incorporated under current policy constraints (Cvitanovic et al., 2014). Here we provide a list of case studies that demonstrate examples of incorporating climate change adaptation into MPA design (Appendix S2).

The second most common barrier is based in governance structures (Figure 5; Cvitanovic et al., 2014; Hagerman & Satterfield, 2014; Hopkins et al., 2016a). This includes cases where policy frameworks and related legislation are not designed to accommodate climate change adaptation. For example, recent updates to MPA policy documents for the European Union do not discuss climate change adaptation (Russel, den Uyl, & de Vito, 2018). Scotland's Marine Act gives reference to how climate change mitigation can be incorporated but does not address adaptation (Hopkins, Bailey, & Potts, 2016b).

Another related barrier concerns uncertainties in legal and regulatory frameworks. Uncertainties in how to incorporate adaptation in management, and rigid government/policy structures have limited the use of adaptive management in MPAs, and this will likely continue (Cvitanovic et al., 2014; Hagerman & Satterfield, 2014; Hopkins et al., 2016a). Legislation and policy structures will need to become much more flexible, and be integrated across different planning and management structures to allow for successful adaptation across the global network of MPAs (Cliquet, 2014; Hopkins et al., 2016a; Spalding et al., 2016). This change has already begun: climate change adaptation is considered in Australia's Marine Park Act (Johnson & Holbrook, 2014; Yates, Clarke, & Thurstan, 2019) and several US policy initiatives are beginning to incorporate climate change adaptation (Petes et al., 2014). Furthermore, theoretical frameworks have been developed which demonstrate how conservation policy could include climate change adaptation (McDonald et al., 2019). Yet, there is still a long way to go to embrace flexible climate-smart planning and management. For instance, dynamic MPAs are a often-cited climate change adaptation strategy in the scientific literature (D'Aloia et al., 2019), but are currently thought to be politically unfeasible in many jurisdictions (Hopkins et al., 2016a; Tittensor et al., 2019).

A third barrier based in governance structures is a mismatch between MPA objectives and definitions of success from regulators and stakeholders' perspectives (Cvitanovic et al., 2014; Hagerman & Satterfield, 2014; Hopkins et al., 2016a). Very few MPAs provide clear objectives that directly relate to climate change (Hopkins et al., 2016a). Unclear objectives make it difficult to evaluate the effectiveness of an MPA with continued climate change which can skew stakeholder perception of success (Hopkins et al., 2016a), although this problem is not specific to climate change objectives (Yates et al., 2019). Clear objectives are needed to ensure the monitoring required for adaptive management is at its most effective (Hopkins et al., 2016a), particularly since the ability to link management actions to objectives is a central tenet of CSC (Stein et al., 2014).

5 | RESEARCH GAPS

In the following, based on our above review, we highlight key research gaps in climate change adaptation for marine conservation planning:

1. *Focus on a variety of ecosystem types across a range of latitudes*. To date almost all studies that consider climate change adaptation have focused on conservation planning for coral reef MPAs. Coral reefs are important ecosystems that are highly vulnerable to climate change (Hoegh-Guldberg et al., 2007). Yet, future work should also focus on developing climate-adaptive MPA designs for more temperate and polar habitats, dominated by other ecosystems or habitat-forming species, such as kelp or seagrass. For instance, the concept of using thermal stress regimes to define the full range of climate heterogeneity is easily transferrable to other biogenic habitats, particularly for climate-sensitive species such as kelp (Wernberg et al., 2016).
2. *Focus on pelagic and deep-sea habitats*. The dominance of corals also meant most research has focused on climate change adaptation in coastal habitats. Climate change impacts will vary in pelagic and deep-sea habitats, which may require new thinking on how adaptation technique should be incorporated into MPAs.
3. *Focus on multiple climate change stressors*. Most vulnerability assessments and corresponding adaptation methods focus primarily on the impact of increasing temperature. While temperature is the most understood impact, increasing temperature will interact with other climate and non-climatic stressors in MPAs potentially resulting in synergistic impacts (Hewitt, Ellis, & Thrush, 2016).
4. *Examine the dichotomy between adaptation strategy recommendations*. Polarizing advice has been provided in the scientific literature by either protecting only climate refugia or protecting the whole range of climate futures (increase heterogeneity), with the former focused on protecting the status quo, and the latter focused on facilitating adaptation. As such:
5. *Gather empirical evidence for the effectiveness of different adaptation strategies*. So far, very few existing MPAs have incorporated climate change adaptation strategies (Tittensor et al., 2019). Therefore, in most cases it is too early to tell which adaptation strategies are the most effective. Experimental research into climate-adaptive MPAs, as well as terrestrial PAs, can help determine which adaptation strategies are the most effective at protecting biodiversity in the face of climate change.

6 | CONCLUSION

Our review provides a comprehensive synthesis of planning frameworks, case studies, adaptation strategies and management actions that can be used to incorporate climate change adaptation into the design and management of MPAs. As there is a vast amount of research on this topic, we can only summarize the main themes, but we have compiled a database of relevant papers to provide further guidance (Appendix S3). This is compiled from the primary literature and does not include all grey literature reports. To address this issue, it has been recommended to create a centralized catalogue of all case studies where climate change adaption has been incorporated into MPA design and management (Tittensor et al., 2019). From the onset of MPA planning, clear conservation goals should be defined, based on both species-based (fine-filter) and higher level (coarse-filter) conservation features. Vulnerability assessments for all conservation features and multiple climate change impacts can provide insight into how species and communities may be impacted, and which specific climate change adaptation strategies should be incorporated into MPA design. MPAs should be closely monitored with relevant indicators and managed adaptively in response to monitoring results. Incorporating climate change adaptation strategies across every stage of the planning process maximizes the likelihood that MPAs will effectively protect marine biodiversity in a changing climate. The outlined conservation planning process, if implemented in existing and future MPAs and networks across the global seascape, could guide a more coordinated effort across nations to protect an increasing number of species and ecosystems (e.g. 30% by 2030) in the face of continued climate change.

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REFERENCES

Abrahms, B., DiPietro, D., Graffis, A., & Hollander, A. (2017). Managing biodiversity under climate change: Challenges, frameworks, and tools for adaptation. *Biodiversity Conservation*, *26*(10), 2277–2293. https://doi.org/10.1007/s10531-017-1362-4

Allnutt, T. F., McClanahan, T. R., Andréfouët, S., Baker, M., Lagabrielle, E., McClennen, C., … Kremen, C. (2012). Comparison of marine spatial planning methods in Madagascar demonstrates value of alternative approaches. *PLoS ONE*, *7*(2), e28969. https://doi.org/10.1371/journal.pone.0028969

Álvarez-Romero, J. G., Mills, M., Adams, V. M., Gurney, G. G., Pressey, R. L., Weeks, R., … Storlie, C. J. (2018). Research advances and gaps in marine planning: Towards a global database in systematic conservation planning. *Biological Conservation*, *227*, 369–382. https://doi.org/10.1016/j.biocon.2018.06.027

Álvarez-Romero, J. G., Munguía-Vega, A., Beger, M., Mar Mancha-Cisneros, M., Suárez-Castillo, A. N., Gurney, G. G., … Torre, J. (2018). Designing connected marine reserves in the face of global warming. *Global Change Biology*, *24*(2), e671–e691. https://doi.org/10.1111/gcb.13989

Andrello, M., Mouillot, D., Somot, S., Thuiller, W., & Manel, S. (2015). Additive effects of climate change on connectivity between marine protected areas and larval supply to fished areas. *Diversity and Distributions*, *21*(2), 139–150. https://doi.org/10.1111/ddi.12250

Ban, N. C., Adams, V. M., Almany, G. R., Ban, S., Cinner, J. E., McCook, L. J., … White, A. (2011). Designing, implementing and managing marine protected areas: Emerging trends and opportunities for coral reef nations. *Journal of Experimental Marine Biology and Ecology*, *408*(1–2), 21–31. https://doi.org/10.1016/j.jembe.2011.07.023

Ban, N. C., Pressey, R. L., & Weeks, S. (2012). Conservation objectives and sea-surface temperature anomalies in the Great Barrier Reef. *Conservation Biology*, *26*(5), 799–809. https://doi.org/10.1111/j.1523-1739.2012.01894.x

Ban, S. S., Alidina, H. M., Okey, T. A., Gregg, R. M., & Ban, N. C. (2016). Identifying potential marine climate change refugia: A case study in Canada's Pacific marine ecosystems. *Global Ecology and Conservation*, *8*, 41–54. https://doi.org/10.1016/j.gecco.2016.07.004

Baron, J. S., Gunderson, L., Allen, C. D., Fleishman, E., McKenzie, D., Meyerson, L. A., … Stephenson, N. (2009). Options for national parks and reserves for adapting to climate change. *Environmental Management*, *44*(6), 1033–1042. https://doi.org/10.1007/s00267-009-9296-6

Bates, A. E., Cooke, R. S. C., Duncan, M. I., Edgar, G. J., Bruno, J. F., Benedetti-Cecchi, L., … Stuart-Smith, R. D. (2019). Climate resilience in marine protected areas and the 'Protection Paradox'. *Biological Conservation*, *236*, 305–314. https://doi.org/10.1016/j.biocon.2019.05.005

Beger, M., McGowan, J., Treml, E. A., Green, A. L., White, A. T., Wolff, N. H., … Possingham, H. P. (2015). Integrating regional conservation priorities for multiple objectives into national policy. *Nature Communications*, *6*, 8208. https://doi.org/10.1038/ncomms9208

Beier, P. (2012). Conceptualizing and designing corridors for climate change. *Ecological Restoration*, *30*(4), 312–319. https://doi.org/10.3368/er.30.4.312

Boyd, P. W., Cornwall, C. E., Davison, A., Doney, S. C., Fourquez, M., Hurd, C. L., … McMinn, A. (2016). Biological responses to environmental heterogeneity under future ocean conditions. *Global Change Biology*, *22*, 2633–2650. https://doi.org/10.1111/gcb.13287

Brock, R. J., Kenchington, E., & Martínez-Arroyo, A. (2012). *Scientific guidelines for designing resilient marine protected area networks in a changing climate*. Montreal, Canada: Commission for Environmental Cooperation, 95 pp.

Bruno, J. F., Bates, A. E., Cacciapaglia, C., Pike, E. P., Amstrup, S. C., van Hooidonk, R., … Aronson, R. B. (2018). Climate change threatens the world's marine protected areas. *Nature Climate Change*, *8*(6), 499–503. https://doi.org/10.1038/s41558-018-0149-2

Carr, M. H., Robinson, S. P., Wahle, C., Davis, G., Kroll, S., Murray, S., … Williams, M. (2017). The central importance of ecological spatial connectivity to effective coastal marine protected areas and to meeting the challenges of climate change in the marine environment. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *27*, 6–29. https://doi.org/10.1002/aqc.2800

Chollett, I., Enríquez, S., & Mumby, P. J. (2014). Redefining thermal regimes to design reserves for coral reefs in the face of climate change. *PLoS ONE*, *9*(10), e110634. https://doi.org/10.1371/journal.pone.0110634

Chollett, I., Mumby, P. J., & Cortés, J. (2010). Upwelling areas do not guarantee refuge for coral reefs in a warming ocean. *Marine Ecology Progress Series*, *416*, 47–56. https://doi.org/10.3354/meps08775

Cliquet, A. (2014). International and European law on protected areas and climate change: Need for adaptation or implementation? *Environmental Management*, *54*(4), 720–731. https://doi.org/10.1007/s00267-013-0228-0

Comte, A., & Pendleton, L. H. (2018). Management strategies for coral reefs and people under global environmental change: 25 years of scientific research. *Journal of Environmental Management*, *209*, 462–474. https://doi.org/10.1016/j.jenvman.2017.12.051

Convertino, M., & Valverde, L. J. (2013). Portfolio decision analysis framework for value-focused ecosystem management. *PLoS ONE*, *8*(6), e65056. https://doi.org/10.1371/journal.pone.0065056

Côté, I. M., & Darling, E. S. (2010). Rethinking ecosystem resilience in the face of climate change. *PLoS Biology*, *8*(7), e1000438. https://doi.org/10.1371/journal.pbio.1000438

Cross, M. S., Zavaleta, E. S., Bachelet, D., Brooks, M. L., Enquist, C. A. F., Fleishman, E., … Tabor, G. M. (2012). The adaptation for conservation targets (ACT) framework: A tool for incorporating climate change into natural resource management. *Environmental Management*, *50*(3), 341–351. https://doi.org/10.1007/s00267-012-9893-7

Cvitanovic, C., Marshall, N. A., Wilson, S. K., Dobbs, K., & Hobday, A. J. (2014). Perceptions of Australian marine protected area managers regarding the role, importance, and achievability of adaptation for managing the risks of climate change. *Ecology and Society*, *19*(4), 33. https://doi.org/10.5751/ES-07019-190433

D'Aloia, C. C., Naujokaitis-Lewis, I., Blackford, C., Chu, C., Curtis, J. M. R., Darling, E., … Fortin, M.-J. (2019). Coupled networks of permanent protected areas and dynamic conservation areas for biodiversity conservation under climate change. *Frontiers in Ecology and Evolution*, *7*, 27. https://doi.org/10.3389/fevo.2019.00027

Davies, H. N., Beckley, L. E., Kobryn, H. T., Lombard, A. T., Radford, B., & Heyward, A. (2016). Integrating climate change resilience features into the incremental refinement of an existing marine park. *PLoS ONE*, *11*(8), e0161094. https://doi.org/10.1371/journal.pone.0161094

Dawson, T. P., Jackson, S. T., House, J. I., Prentice, I. C., & Mace, G. M. (2011). Beyond predictions: Biodiversity conservation in a changing climate. *Science*, *332*(6025), 53–58. https://doi.org/10.1126/science.1200303

Delevaux, J. M. S., Jupiter, S. D., Stamoulis, K. A., Bremer, L. L., Wenger, A. S., Dacks, R., … Ticktin, T. (2018). Scenario planning with linked land-sea models inform where forest conservation actions will promote coral reef resilience. *Scientific Reports*, *8*, 12465. https://doi.org/10.1038/s41598-018-29951-0

Delevaux, J. M. S., Stamoulis, K. A., Whittier, R., Jupiter, S. D., Bremer, L. L., Friedlander, A., … Ticktin, T. (2019). Place-based management can reduce human impacts on coral reefs in a changing climate. *Ecological Applications*, *29*(4), e01891. https://doi.org/10.1002/eap.1891

Foden, W. B., Young, B. E., Akçakaya, H. R., Garcia, R. A., Hoffmann, A. A., Stein, B. A., … Huntley, B. (2019). Climate change vulnerability assessment of species. *Wiley Interdisciplinary Reviews: Climate Change*, *10*, e551. https://doi.org/10.1002/wcc.551

Foley, M. M., Halpern, B. S., Micheli, F., Armsby, M. H., Caldwell, M. R., Crain, C. M., … Steneck, R. S. (2010). Guiding ecological principles for marine spatial planning. *Marine Policy*, *34*(5), 955–966. https://doi.org/10.1016/j.marpol.2010.02.001

Fredston-Hermann, A., Gaines, S. D., & Halpern, B. S. (2018). Biogeographic constraints to marine conservation in a changing climate. *Annals of the New York Academy of Sciences*, *1429*, 5–17. https://doi.org/10.1111/nyas.13597

Friesen, S. K., Martone, R., Rubidge, E., Baggio, J. A., & Ban, N. C. (2019). An approach to incorporating inferred connectivity of adult movement into marine protected area design with limited data. *Ecological Applications*, *29*, e01890. https://doi.org/10.1002/eap.1890

Game, E. T., Bode, M., McDonald-Madden, E., Grantham, H. S., & Possingham, H. P. (2009). Dynamic marine protected areas can improve the resilience of coral reef systems. *Ecology Letters*, *12*(12), 1336–1345. https://doi.org/10.1111/j.1461-0248.2009.01384.x

Game, E. T., McDonald-Madden, E., Puotinen, M. L., & Possingham, H. P. (2008). Should we protect the strong or the weak? Risk, resilience, and the selection of marine protected areas. *Conservation Biology*, *22*(6), 1619–1629. https://doi.org/10.1111/j.1523-1739.2008.01037.x

Game, E. T., Watts, M. E., Wooldridge, S., & Possingham, H. P. (2008). Planning for persistence in marine reserves: A question of catastrophic importance. *Ecological Applications*, *18*(3), 670–680. https://doi.org/10.1890/07-1027.1

Gerber, L. R., Mancha-Cisneros, M. D. M., O'Connor, M. I., & Selig, E. R. (2014). Climate change impacts on connectivity in the ocean: Implications for conservation. *Ecosphere*, *5*(3), 33. https://doi.org/10.1890/ES13-00336.1

Gibbin, E. M., Putnam, H. M., Gates, R. D., Nitschke, M. R., & Davy, S. K. (2015). Species-specific differences in thermal tolerance may define susceptibility to intracellular acidosis in reef corals. *Marine Biology*, *162*(3), 717–723. https://doi.org/10.1007/s00227-015-2617-9

Gill, D. A., Mascia, M. B., Ahmadia, G. N., Glew, L., Lester, S. E., Barnes, M., … Fox, H. E. (2017). Capacity shortfalls hinder the performance of marine protected areas globally. *Nature*, *543*(7647), 665–669. https://doi.org/10.1038/nature21708

Green, A. L., Fernandes, L., Almany, G., Abesamis, R., McLeod, E., Aliño, P. M., … Pressey, R. L. (2014). Designing marine reserves for fisheries management, biodiversity conservation, and climate change adaptation. *Coastal Management*, *42*(2), 143–159. https://doi.org/10.1080/08920753.2014.877763

Green, A., Smith, S. E., Lipsett-Moore, G., Groves, C., Peterson, N., Sheppard, S., … Bualia, L. (2009). Designing a resilient network of marine protected areas for Kimbe Bay, Papua New Guinea. *Oryx*, *43*(4), 488–498. https://doi.org/10.1017/S0030605309990342

Gross, J., Woodley, S., Welling, L. A., & Watson, J. E. M. (2016). *Adapting to climate change: Guidance for protected area managers and planners. Best practice protected area guidelines series no. 24*. Gland, Switzerland: IUCN. xviii + 129 pp.

Gurney, G. G., Melbourne-Thomas, J., Geronimo, R. C., Aliño, P. M., & Johnson, C. R. (2013). Modelling coral reef futures to inform management: Can reducing local-scale stressors conserve reefs under climate change? *PLoS ONE*, *8*, e80137. https://doi.org/10.1371/journal.pone.0080137

Hagerman, S. M., & Satterfield, T. (2014). Agreed but not preferred: Expert views on taboo options for biodiversity conservation, given climate change. *Ecological Applications*, *24*(3), 548–559. https://doi.org/10.1890/13-0400.1

Hannah, L. (2008). Protected areas and climate change. *Annals of the New York Academy of Sciences*, *1134*, 201–212. https://doi.org/10.1196/annals.1439.009

Hannah, L. (2010). A global conservation system for climate-change adaptation: Special section. *Conservation Biology*, *24*(1), 70–77. https://doi.org/10.1111/j.1523-1739.2009.01405.x

Hannah, L., Midgley, G. F., & Millar, D. (2002). Climate change-integrated conservation strategies. *Global Ecology & Biogeography*, *11*, 485–495. https://doi.org/10.1046/j.1466-822X.2002.00306.x

Heller, N. E., & Zavaleta, E. S. (2009). Biodiversity management in the face of climate change: A review of 22 years of recommendations. *Biological Conservation*, *142*(1), 14–32. https://doi.org/10.1016/j.biocon.2008.10.006

Hewitt, J. E., Ellis, J. I., & Thrush, S. F. (2016). Multiple stressors, nonlinear effects and the implications of climate change impacts on marine coastal ecosystems. *Global Change Biology*, *22*(8), 2665–2675. https://doi.org/10.1111/gcb.13176

Hobday, A. J. (2011). Sliding baselines and shuffling species: Implications of climate change for marine conservation. *Marine Ecology*, *32*(3), 392–403. https://doi.org/10.1111/j.1439-0485.2011.00459.x

Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E., … Hatziolos, M. E. (2007). Coral reefs under rapid climate change and ocean acidification. *Science*, *318*(5857), 1737–1742. https://doi.org/10.1126/science.1152509

Holling, C. S. (1973). Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*, *4*, 1–23. https://doi.org/10.1146/annurev.es.04.110173.000245

Hopkins, C. R., Bailey, D. M., & Potts, T. (2016a). Perceptions of practitioners: Managing marine protected areas for climate change resilience. *Ocean and Coastal Management*, *128*, 18–28. https://doi.org/10.1016/j.ocecoaman.2016.04.014

Hopkins, C. R., Bailey, D. M., & Potts, T. (2016b). Scotland's marine protected area network: Reviewing progress towards achieving commitments for marine conservation. *Marine Policy*, *71*, 44–53. https://doi.org/10.1016/j.marpol.2016.05.015

IPBES. (2019). *Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services* (S. Díaz, J. Settele, E. S. Brondízio, H. T. Ngo, M. Guèze, J. Agard, … C. N. Zayas, Eds.). Bonn, Germany: IPBES Secretariat, 56 pp.

IPCC. (2019). Summary for policymakers. In H.-O. Pörtner, D. C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, … N. M. Weyer (Eds.), *IPCC special report on the ocean and cryosphere in a changing climate*, in press.

Johnson, J. E., & Holbrook, N. J. (2014). Adaptation of Australia's marine ecosystems to climate change: Using science to inform conservation management. *International Journal of Ecology*, *2014*, 1–12. https://doi.org/10.1155/2014/140354

Jones, K. R., Watson, J. E. M., Possingham, H. P., & Klein, C. J. (2016). Incorporating climate change into spatial conservation prioritisation: A review. *Biological Conservation*, *194*, 121–130. https://doi.org/10.1016/j.biocon.2015.12.008

Jones, M. C., Dye, S. R., Fernandes, J. A., Frölicher, T. L., Pinnegar, J. K., Warren, R., & Cheung, W. W. L. (2013). Predicting the impact of climate change on threatened species in UK waters. *PLoS ONE*, *8*(1), e54216. https://doi.org/10.1371/journal.pone.0054216

Kay, S., & Butenschön, M. (2018). Projections of change in key ecosystem indicators for planning and management of marine protected areas: An example study for European seas. *Estuarine, Coastal and Shelf Science*, *201*, 172–184. https://doi.org/10.1016/j.ecss.2016.03.003

Keller, B. D., Gleason, D. F., McLeod, E., Woodley, C. M., Airamé, S., Causey, B. D., … Steneck, R. S. (2009). Climate change, coral reef ecosystems, and management options for marine protected areas. *Environmental Management*, *44*(6), 1069–1088. https://doi.org/10.1007/s00267-009-9346-0

Keppel, G., Mokany, K., Wardell-Johnson, G. W., Phillips, B. L., Welbergen, J. A., & Reside, A. E. (2015). The capacity of refugia for conservation planning under climate change. *Frontiers in Ecology and the Environment*, *13*(2), 106–112. https://doi.org/10.1890/140055

Klein, C. J., Tulloch, V. J., Halpern, B. S., Selkoe, K. A., Watts, M. E., Steinback, C., … Possingham, H. P. (2013). Tradeoffs in marine reserve design: Habitat condition, representation, and socioeconomic costs. *Conservation Letters*, *6*(5), 324–332. https://doi.org/10.1111/conl.12005

Kujala, H., Moilanen, A., Araújo, M. B., & Cabeza, M. (2013). Conservation planning with uncertain climate change projections. *PLoS ONE*, *8*, e53315. https://doi.org/10.1371/journal.pone.0053315

Kwiatkowski, L., Halloran, P. R., Mumby, P. J., & Stephenson, D. B. (2014). What spatial scales are believable for climate model projections of sea surface temperature? *Climate Dynamics*, *43*, 1483–1496. https://doi.org/10.1007/s00382-013-1967-6

Lemieux, C. J., Groulx, M. W., Bocking, S., & Beechey, T. J. (2018). Evidence-based decision-making in Canada's protected areas organizations: Implications for management effectiveness. *Factes*, *3*, 392–414.

Levy, J. S., & Ban, N. C. (2013). A method for incorporating climate change modelling into marine conservation planning: An Indo-west Pacific example. *Marine Policy*, *38*, 16–24. https://doi.org/10.1016/j.marpol.2012.05.015

Lombard, A. T., Reyers, B., Schonegevel, L. Y., Cooper, J., Smith-Adao, L. B., Nel, D. C., … Chown, S. L. (2007). Conserving pattern and process in the Southern Ocean: Designing a marine protected area for the prince Edward Islands. *Antarctic Science*, *19*(1), 39–54. https://doi.org/10.1017/s0954102007000077

Lotze, H. K., Tittensor, D. P., Bryndum-Buchholz, A., Eddy, T. D., Cheung, W. W. L., Galbraith, E. D., … Worm, B. (2019). Global ensemble projections reveal trophic amplification of ocean biomass declines with climate change. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(26), 12907–12912. https://doi.org/10.1073/pnas.1900194116

Lubchenco, J., & Grorud-Colvert, K. (2015). Making waves: The science and politics of ocean protection. *Science*, *350*(6259), 382–383. https://doi.org/10.1017/CBO9781107415324.004

Ma, X. (2018). Governing marine protected areas in a changing climate: Private stakeholders' perspectives. *Arctic Review on Law and Politics*, *9*, 335–358. https://doi.org/10.23865/arctic.v9.1208

Macgregor, N. A., & van Dijk, N. (2014). Adaptation in practice: How managers of nature conservation areas in Eastern England are responding to climate change. *Environmental Management*, *54*(4), 700–719. https://doi.org/10.1007/s00267-014-0254-6

Mach, M. E., Wedding, L. M., Reiter, S. M., Micheli, F., Fujita, R. M., & Martone, R. G. (2017). Assessment and management of cumulative impacts in California's network of marine protected areas. *Ocean and Coastal Management*, *137*, 1–11. https://doi.org/10.1016/j.ocecoaman.2016.11.028

Mačić, V., Albano, P. G., Almpanidou, V., Claudet, J., Corrales, X., Essl, F., … Katsanevakis, S. (2018). Biological invasions in conservation planning: A global systematic review. *Frontiers in Marine Science*, *5*, 178. https://doi.org/10.3389/fmars.2018.00178

Magris, R. A., Heron, S. F., & Pressey, R. L. (2015). Conservation planning for coral reefs accounting for climate warming disturbances. *PLoS ONE*, *10*(11), e0140828. https://doi.org/10.1371/journal.pone.0140828

Magris, R. A., Pressey, R. L., Mills, M., Vila-Nova, D. A., & Floeter, S. (2017). Integrated conservation planning for coral reefs: Designing conservation zones for multiple conservation objectives in spatial prioritisation. *Global Ecology and Conservation*, *11*, 53–68. https://doi.org/10.1016/j.gecco.2017.05.002

Magris, R. A., Pressey, R. L., Weeks, R., & Ban, N. C. (2014). Integrating connectivity and climate change into marine conservation planning. *Biological Conservation*, *170*, 207–221. https://doi.org/10.1016/j.biocon.2013.12.032

Maina, J. M., Jones, K. R., Hicks, C. C., McClanahan, T. R., Watson, J. E. M., Tuda, A. O., & Andréfouët, S. (2015). Designing climate-resilient marine protected area networks by combining remotely sensed coral reef habitat with coastal multi-use maps. *Remote Sensing*, *7*(12), 16571–16587. https://doi.org/10.3390/rs71215849

Makino, A., Klein, C. J., Possingham, H. P., Yamano, H., Yara, Y., Ariga, T., … Beger, M. (2015). The effect of applying alternate IPCC climate scenarios to marine reserve design for range changing species. *Conservation Letters*, *8*(5), 320–328. https://doi.org/10.1111/conl.12147

Makino, A., Yamano, H., Beger, M., Klein, C. J., Yara, Y., & Possingham, H. P. (2014). Spatio-temporal marine conservation planning to support high-latitude coral range expansion under climate change. *Diversity and Distributions*, *20*(8), 859–871. https://doi.org/10.1111/ddi.12184

Malcolm, H. A., & Ferrari, R. (2019). Strong fish assemblage patterns persist over sixteen years in a warming marine park, even with tropical shifts. *Biological Conservation*, *232*, 152–163. https://doi.org/10.1016/j.biocon.2019.02.005

Mangubhai, S., Wilson, J. R., Rumetna, L., Maturbongs, Y., & Purwanto (2015). Explicitly incorporating socioeconomic criteria and data into marine protected area zoning. *Ocean and Coastal Management*, *116*, 523–529. https://doi.org/10.1016/j.ocecoaman.2015.08.018

Margules, C. R., & Pressey, R. L. (2000). Systematic conservation planning. *Nature*, *405*(6783), 243–253. https://doi.org/10.1038/35012251

Mawdsley, J. R., O'Malley, R., & Ojima, D. S. (2009). A review of climate-change adaptation strategies for wildlife management and biodiversity conservation. *Conservation Biology*, *23*(5), 1080–1089. https://doi.org/10.1111/j.1523-1739.2009.01264.x

Maxwell, S. L., Venter, O., Jones, K. R., & Watson, J. E. M. (2015). Integrating human responses to climate change into conservation vulnerability assessments and adaptation planning. *Annals of the New York Academy of Sciences*, *1355*(1), 98–116. https://doi.org/10.1111/nyas.12952

Maynard, J. A., Marshall, P. A., Johnson, J. E., & Harman, S. (2010). Building resilience into practical conservation: Identifying local management responses to global climate change in the southern Great Barrier Reef. *Coral Reefs*, *29*(2), 381–391. https://doi.org/10.1007/s00338-010-0603-8

McCook, L. J., Almany, G. R., Berumen, M. L., Day, J. C., Green, A. L., Jones, G. P., … Thorrold, S. R. (2009). Management under uncertainty: Guidelines for incorporating connectivity into the protection of coral reefs. *Coral Reefs*, *28*(2), 353–366. https://doi.org/10.1007/s00338-008-0463-7

McCook, L. J., Ayling, T., Cappo, M., Choat, J. H., Evans, R. D., De Freitas, D. M., … Williamson, D. H. (2010). Adaptive management of the Great Barrier Reef: A globally significant demonstration of the benefits of networks of marine reserves. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(43), 18278–18285. https://doi.org/10.1073/pnas.0909335107

McDonald, J., McCormack, P. C., Dunlop, M., Farrier, D., Feehely, J., Gilfedder, L., … Reside, A. E. (2019). Adaptation pathways for conservation law and policy. *Wiley Interdisciplinary Reviews: Climate Change*, *10*(1), e555. https://doi.org/10.1002/wcc.555

Mcleod, E., Anthony, K. R. N., Mumby, P. J., Maynard, J., Beeden, R., Graham, N. A. J., … Tamelander, J. (2019). The future of resilience-based management in coral reef ecosystems. *Journal of Environmental Management*, *233*, 291–301. https://doi.org/10.1016/j.jenvman.2018.11.034

McLeod, E., Green, A., Game, E., Anthony, K., Cinner, J., Heron, S. F., … Woodroffe, C. (2012). Integrating climate and ocean change vulnerability into conservation planning. *Coastal Management*, *40*(6), 651–672. https://doi.org/10.1080/08920753.2012.728123

McLeod, E., Salm, R. V., Green, A. L., & Almany, J. (2009). Designing marine protected area networks to address the impacts of climate change. *Frontiers in Ecology and the Environment*, *7*(7), 362–370. https://doi.org/10.1890/070211

Micheli, F., Saenz-Arroyo, A., Greenley, A., Vazquez, L., Espinoza Montes, J. A., Rossetto, M., & De Leo, G. A. (2012). Evidence that marine reserves enhance resilience to climatic impacts. *PLoS ONE*, *7*(7), e40832. https://doi.org/10.1371/journal.pone.0040832

Mumby, P. J., Elliott, I. A., Eakin, C. M., Skirving, W., Paris, C. B., Edwards, H. J., … Stevens, J. R. (2011). Reserve design for uncertain responses of coral reefs to climate change. *Ecology Letters*, *14*(2), 132–140. https://doi.org/10.1111/j.1461-0248.2010.01562.x

Mumby, P. J., Wolff, N. H., Bozec, Y., Chollett, I., & Halloran, P. (2014). Operationalizing the resilience of coral reefs in an era of climate change. *Conservation Letters*, *7*, 176–187. https://doi.org/10.1111/conl.12047

Munday, P. L., Leis, J. M., Lough, J. M., Paris, C. B., Kingsford, M. J., Berumen, M. L., & Lambrechts, J. (2009). Climate change and coral reef connectivity. *Coral Reefs*, *28*(2), 379–395. https://doi.org/10.1007/s00338-008-0461-9

Munguia-Vega, A., Green, A. L., Suarez-Castillo, A. N., Espinosa-Romero, M. J., Aburto-Oropeza, O., Cisneros-Montemayor, A. M., … Weaver, A. H. (2018). Ecological guidelines for designing networks of marine reserves in the unique biophysical environment of the Gulf of California. *Reviews in Fish Biology and Fisheries*, *28*(4), 749–776. https://doi.org/10.1007/s11160-018-9529-y

Nyström, M., & Folke, C. (2001). Spatial Resilience of coral reefs. *Ecosystems*, *4*(5), 406–417. https://doi.org/10.1007/s10021-001-0019-y

Olds, A. D., Connolly, R. M., Pitt, K. A., Pittman, S. J., Maxwell, P. S., Huijbers, C. M., … Schlacher, T. A. (2016). Quantifying the conservation value of seascape connectivity: A global synthesis. *Global Ecology and Biogeography*, *25*(1), 3–15. https://doi.org/10.1111/geb.12388

Otero, M., Garrabou, J., & Vargas, M. (2013). *Mediterranean marine protected areas and climate change: A guide to regional monitoring and adaptation opportunities*. Malaga, Spain: IUCN, 52 pp.

Pacifici, M., Foden, W. B., Visconti, P., Watson, J. E. M., Butchart, S. H. M., Kovacs, K. M., … Rondinini, C. (2015). Assessing species vulnerability to climate change. *Nature Climate Change*, *5*(3), 215–225. https://doi.org/10.1038/nclimate2448

Patrizzi, N. S., & Dobrovolski, R. (2018). Integrating climate change and human impacts into marine spatial planning: A case study of threatened starfish species in Brazil. *Ocean & Coastal Management*, *161*, 177–188. https://doi.org/10.1016/j.ocecoaman.2018.05.003

Perdanahardja, G., & Lionata, H. (2017). *Nine years in lesser sunda*. Indonesia: The Nature Conservancy, Indonesia Coasts and Oceans Program, 127 pp.

Petes, L. E., Howard, J. F., Helmuth, B. S., & Fly, E. K. (2014). Science integration into US climate and ocean policy. *Nature Climate Change*, *4*(8), 671–677. https://doi.org/10.1038/nclimate2312

Poiani, K. A., Goldman, R. L., Hobson, J., Hoekstra, J. M., & Nelson, K. S. (2011). Redesigning biodiversity conservation projects for climate change: Examples from the field. *Biodiversity and Conservation*, *20*(1), 185–201. https://doi.org/10.1007/s10531-010-9954-2

Poloczanska, E. S., Burrows, M. T., Brown, C. J., García Molinos, J., Halpern, B. S., Hoegh-Guldberg, O., … Sydeman, W. J. (2016). Responses of marine organisms to climate change across oceans. *Frontiers in Marine Science*, *3*, 62. https://doi.org/10.3389/fmars.2016.00062

Queirós, A. M., Huebert, K. B., Keyl, F., Fernandes, J. A., Stolte, W., Maar, M., … Peck, M. A. (2016). Solutions for ecosystem-level protection of ocean systems under climate change. *Global Change Biology*, *22*(12), 3927–3936. https://doi.org/10.1111/gcb.13423

Rannow, S., Macgregor, N. A., Albrecht, J., Crick, H. Q. P., Förster, M., Heiland, S., … Sienkiewicz, J. (2014). Managing protected areas under climate change: Challenges and priorities. *Environmental Management*, *54*(4), 732–743. https://doi.org/10.1007/s00267-014-0271-5

Reside, A. E., Butt, N., & Adams, V. M. (2018). Adapting systematic conservation planning for climate change. *Biodiversity and Conservation*, *27*(1), 1–29. https://doi.org/10.1007/s10531-017-1442-5

Rilov, G., Mazaris, A. D., Stelzenmüller, V., Helmuth, B., Wahl, M., Guy-Haim, T., … Katsanevakis, S. (2019). Adaptive marine conservation planning in the face of climate change: What can we learn from physiological, ecological and genetic studies? *Global Ecology and Conservation*, *17*, e00566. https://doi.org/10.1016/j.gecco.2019.e00566

Roberts, C. M., Halpern, B., Palumbi, S. R., & Warner, R. R. (2001). Designing marine reserve networks why small, isolated protected areas are not enough. *Conservation in Practice*, *2*(3), 10–17. https://doi.org/10.1111/j.1526-4629.2001.tb00012.x

Roberts, C. M., O'Leary, B. C., McCauley, D. J., Cury, P. M., Duarte, C. M., Lubchenco, J., … Castilla, J. C. (2017). Marine reserves can mitigate and promote adaptation to climate change. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(24), 6167–6175. https://doi.org/10.1073/pnas.1701262114

Robinson, L. M., Elith, J., Hobday, A. J., Pearson, R. G., Kendall, B. E., Possingham, H. P., & Richardson, A. J. (2011). Pushing the limits in marine species distribution modelling: Lessons from the land present challenges and opportunities. *Global Ecology and Biogeography*, *20*(6), 789–802. https://doi.org/10.1111/j.1466-8238.2010.00636.x

Rogers, A., Harborne, A. R., Brown, C. J., Bozec, Y.-M., Castro, C., Chollett, I., … Mumby, P. J. (2015). Anticipative management for coral reef ecosystem services in the 21st century. *Global Change Biology*, *21*(2), 504–514. https://doi.org/10.1111/gcb.12725

Runting, R. K., Wilson, K. A., & Rhodes, J. R. (2013). Does more mean less? The value of information for conservation planning under sea level rise. *Global Change Biology*, *19*(2), 352–363. https://doi.org/10.1111/gcb.12064

Russel, D. J., den Uyl, R. M., & de Vito, L. (2018). Understanding policy integration in the EU – Insights from a multi-level lens on climate adaptation and the EU's coastal and marine policy. *Environmental Science and Policy*, *82*, 44–51. https://doi.org/10.1016/j.envsci.2017.12.009

Salm, R. V., Done, T., & McLeod, E. (2006). Marine protected area planning in a changing climate. In J. T. Phinney, O. Hoegh-Guldberg, J. Kleypas, W. Skirving, & A. Strong (Eds.), *Coral reefs and climate change: Science and management* (pp. 207–221). Washington, DC: American Geophysical Union.

Schneider, C. L. (2018). Marine refugia past, present, and future: Lessons from ancient geologic crises for modern marine ecosystem conservation. In C. Tyler & C. Schneider (Eds.). *Marine conservation paleobiology. Topics in geobiology* (Vol. *47*, pp. 163–208). Cham, Switzerland: Springer.

Selig, E. R., Casey, K. S., & Bruno, J. F. (2012). Temperature-driven coral decline: The role of marine protected areas. *Global Change Biology*, *18*(5), 1561–1570. https://doi.org/10.1111/j.1365-2486.2012.02658.x

Simard, F., Laffoley, D., & Baxter, J. M. (Eds.). (2016). *Marine protected areas and climate change: Adaptation and mitigation synergies, opportunities and challenges*. Gland, Switzerland: IUCN, 52 pp.

Soto, C. G. (2002). The potential impacts of global climate change on marine protected areas. *Reviews in Fish Biology and Fisheries*, *11*(3), 181–195. https://doi.org/10.1023/A:1020364409616

Spalding, M. D., Meliane, I., Bennett, N. J., Dearden, P., Patil, P. G., & Brumbaugh, R. D. (2016). Building towards the marine conservation end-game: Consolidating the role of MPAs in a future ocean. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *26*, 185–199. https://doi.org/10.1002/aqc.2686

Stein, B. A., Glick, P., Edelson, N., & Staudg, A. (2014). *Climate-smart conservation: Putting adaptation principles into practice*. Washington, DC: National Wildlife Federation.

Stratoudakis, Y., Hilário, A., Ribeiro, C., Abecasis, D., Gonçalves, E. J., Andrade, F., … Henriques, S. (2019). Environmental representativity in marine protected area networks over large and partly unexplored seascapes. *Global Ecology and Conservation*, *17*, e00545. https://doi.org/10.1016/j.gecco.2019.e00545

Timpane-Padgham, B. L., Beechie, T., & Klinger, T. (2017). A systematic review of ecological attributes that confer resilience to climate change in environmental restoration. *PLoS ONE*, *12*(3), e0173812. https://doi.org/10.1371/journal.pone.0173812

Tingley, M. W., Darling, E. S., & Wilcove, D. S. (2014). Fine- and coarse-filter conservation strategies in a time of climate change. *Annals of the New York Academy of Sciences*, *1322*(1), 92–109. https://doi.org/10.1111/nyas.12484

Tittensor, D. P., Beger, M., Böerder, K., Boyce, D., Cavanagh, R., Cosandey-Godin, A., … Worm, B. (2019). Integrating climate adaptation and biodiversity conservation in the global protected ocean. *Science Advances*, *5*(11), eaay9969.

Tuda, A. O., & Machumu, M. E. (2019). Institutions and adaptive capacity for marine biodiversity conservation. *Environmental Science and Policy*, *100*, 238–246. https://doi.org/10.1016/j.envsci.2019.03.012

UNEP-WCMC, IUCN, & NGS. (2018). *Protected planet report 2018*. Cambridge UK; Gland, Switzerland; and Washington, DC: Author, 56 pp.

van Hooidonk, R., Maynard, J. A., Liu, Y., & Lee, S.-K. (2015). Downscaled projections of Caribbean coral bleaching that can inform conservation planning. *Global Change Biology*, *21*, 3389–3401. https://doi.org/10.1111/gcb.12901

Walsworth, T. E., Schindler, D. E., Colton, M. A., Webster, M. S., Palumbi, S. R., Mumby, P. J., … Pinsky, M. L. (2019). Management for network diversity speeds evolutionary adaptation to climate change. *Nature Climate Change*, *9*, 632–636. https://doi.org/10.1038/s41558-019-0518-5

Webster, M. S., Colton, M. A., Darling, E. S., Armstrong, J., Pinsky, M. L., Knowlton, N., & Schindler, D. E. (2017). Who should pick the winners of climate change? *Trends in Ecology & Evolution*, *32*(3), 167–173. https://doi.org/10.1016/j.tree.2016.12.007

Weeks, R., & Jupiter, S. D. (2013). Adaptive comanagement of a marine protected area network in Fiji. *Conservation Biology*, *27*(6), 1234–1244. https://doi.org/10.1111/cobi.12153

Wenzel, L., Gilbert, N., Goldsworthy, L., Tesar, C., Mcconnell, M., & Okter, M. (2016). Polar opposites? Marine conservation tools and experiences in the changing Arctic and Antarctic. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *26*, 61–84. https://doi.org/10.1002/aqc.2649

Wernberg, T., Bennett, S., Babcock, R. C., de Bettignies, T., Cure, K., Depczynski, M., … Wilson, S. (2016). Climate-driven regime shift of a temperate marine ecosystem. *Science*, *353*(6295), 169–172. https://doi.org/10.1126/science.aad8745

West, J. M., Julius, S. H., Kareiva, P., Enquist, C., Lawler, J. J., Petersen, B., … Shaw, M. R. (2009). U.S. natural resources and climate change: Concepts and approaches for management adaptation. *Environmental Management*, *44*(6), 1001–1021. https://doi.org/10.1007/s00267-009-9345-1

Willis, S. G., Foden, W., Baker, D. J., Belle, E., Burgess, N. D., Carr, J. A., … Butchart, S. (2015). Integrating climate change vulnerability assessments from species distribution models and trait-based approaches. *Biological Conservation*, *190*, 167–178. https://doi.org/10.1016/j.biocon.2015.05.001

Woodson, C. B., Micheli, F., Boch, C., Al-Najjar, M., Espinoza, A., Hernandez, A., … Torre, J. (2019). Harnessing marine microclimates for climate change adaptation and marine conservation. *Conservation Letters*, *12*(2), 1–9. https://doi.org/10.1111/conl.12609

Worm, B., & Lotze, H. K. (2016). Marine biodiversity and climate change. In T. M. Letcher (Ed.), *Climate change: Observed impacts on planet earth* (pp. 195–212). https://doi.org/10.1016/j.marpolbul.2008.05.006

Wyborn, C., van Kerkhoff, L., Dunlop, M., Dudley, N., & Guevara, O. (2016). Future oriented conservation: Knowledge governance, uncertainty and learning. *Biodiversity and Conservation*, *25*(7), 1401–1408. https://doi.org/10.1007/s10531-016-1130-x

Yates, K. L., Clarke, B., & Thurstan, R. H. (2019). Purpose vs performance: What does marine protected area success look like? *Environmental Science and Policy*, *92*, 76–86. https://doi.org/10.1016/j.envsci.2018.11.012

Zupan, M., Fragkopoulou, E., Claudet, J., Erzini, K., Horta e Costa, B., & Gonçalves, E. J. (2018). Marine partially protected areas: Drivers of ecological effectiveness. *Frontiers in Ecology and the Environment*, *16*(7), 381–387. https://doi.org/10.1002/fee.1934

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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