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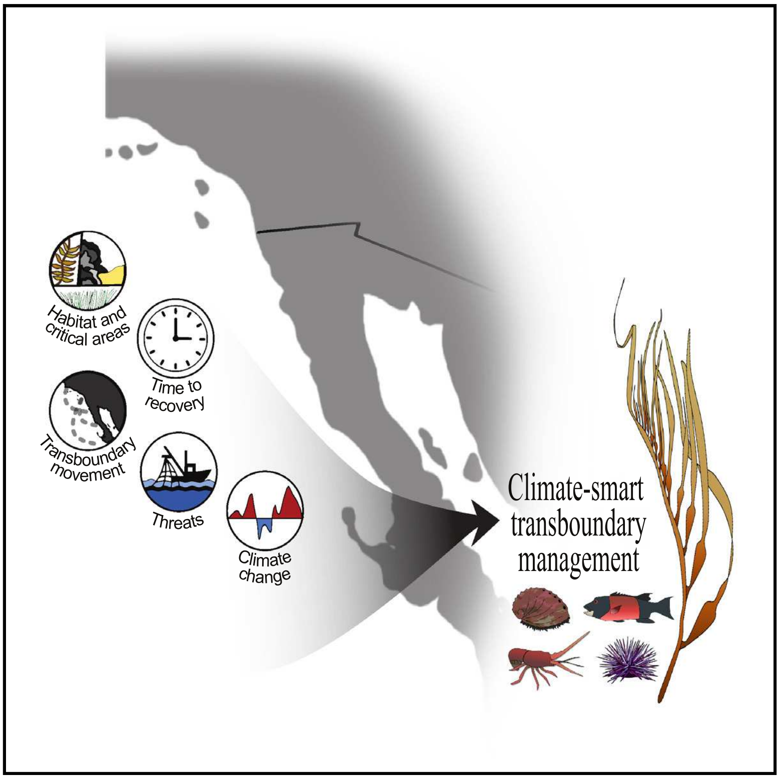
Integrating climate adaptation and transboundary management: Guidelines for designing climate-smart marine protected areas

Graphical abstract



Highlights

- We provide 21 guidelines for designing climate-smart transboundary protected areas
- Future climates could decrease connectivity by 50% and hinder species recovery
- Climate-smart networks require protecting critical sites and climate refugia
- Adapting to climate change requires transboundary coordination in shared ecoregions

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In brief

Climate change is impacting marine biodiversity globally, and the international community recognizes the need to implement climate-adaptation strategies and increase conservation efforts. We provide 21 guidelines for designing climate-smart marine protected areas and recommendations for their application in the transboundary California Bight, a shared ecoregion between the United States and Mexico. With a post-2020 global protection target recently approved, our framework for integrating climate adaptation and transboundary management will help nations' aspirations of protecting 30% of their oceans by 2030.

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Integrating climate adaptation and transboundary management: Guidelines for designing climate-smart marine protected areas

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SCIENCE FOR SOCIETY Protecting nature is an essential measure to support the recovery of biodiversity from the impacts of climate change. For networks of marine protected areas (MPAs) to be climate smart, their design needs to address the vulnerability of biodiversity to current and future climate-change impacts. However, establishing these networks requires transboundary management when species move across international borders. Here, by providing guidelines and recommendations for designing climate-smart transboundary MPAs, we emphasize that nations should increase the coverage of MPAs, protect critical transboundary sites for the future functioning of the network, and protect those places less impacted by climate change. With new global protection targets aiming to preserve 30% of the planet by 2030, our work provides a framework and practical recommendations to guide nations embarking on climate-smart conservation and transboundary management.

SUMMARY

Climate change poses an urgent threat to biodiversity that demands societal responses. The magnitude of this challenge is reflected in recent international commitments to protect 30% of the planet by 2030 while adapting to climate change. However, because climate change is global, interventions must transcend political boundaries. Here, using the California Bight as a case study, we provide 21 biophysical guidelines for designing climate-smart transboundary marine protected area (MPA) networks and conduct analyses to inform their application. We found that future climates and marine heatwaves could decrease ecological connectivity by 50% and hinder the recovery of vulnerable species in MPAs. To buffer the impacts of climate change, MPA coverage should be expanded, focusing on protecting critical nodes for the network and climate refugia, where impacts might be less severe. For shared ecoregions, these actions require international coordination. Our work provides the first comprehensive framework for integrating climate resilience for MPAs in transboundary ecoregions, which will support other nations' aspirations.

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INTRODUCTION

Marine protected areas (MPAs) are the cornerstone of most conservation strategies,[1] and their importance is reflected in the post-2020 global biodiversity framework that was agreed upon at COP15 in December 2022.[2] This international framework calls for protecting 30% of the oceans by 2030[2] through representative and well-connected networks of MPAs and other areas-based conservation measures. Because climate change is one of the main threats to marine ecosystems[3–5] the new framework stipulates the need to include climate adaptation in MPA design and management. Yet, to date, the MPA planning process considers only a few, if any, aspects of climate change.[6] One approach that MPA planners could use is the climate-smart framework, which addresses the vulnerability of species and ecosystems to changes in climate and ocean chemistry and supports the resilience of populations and ecosystems by considering multiple climate-adaptation strategies.[7,8] Climate-adaptation strategies include protecting areas that act as climate refugia,[9–12] maintaining ecological connectivity to ensure metapopulation persistence[13] and facilitating recovery of important species for ecosystem functioning.[14]

Well-managed and restrictive MPAs (marine reserves) rebuild the biomass of overfished species,[15,16] conserve biodiversity,[17] and enhance the resilience and adaptive capacity of ecosystems to climate impacts.[18–23] However, delivering large-scale benefits requires networks of marine reserves that are functionally interconnected and large enough to protect the underlying biophysical processes that maintain species distribution and composition.[24,25] Although a rich literature exists on biophysical guidelines for designing networks of marine reserves,[26–28] most are limited to analyses within national boundaries. By contrast, ecoregion-scale planning efforts may span thousands of kilometers and, in many cases, cross multiple national or international jurisdictions.[29–31] Consequently, before designing networks of marine reserves, planners need to develop shared biophysical guidelines and comprehensive spatial analyses across borders.[32,33]

Biophysical guidelines for a reserve system fall into six major categories: (1) ensuring habitat representation and replication; (2) protecting critical and unique areas; (3) incorporating connectivity; (4) allowing time for recovery; (5) minimizing and avoiding local threats; and (6) adapting to climate change[26–28,34,35] (see Note S1 for more details). Although existing guidelines acknowledge the need for climate-change adaptation,[26,27] they provide general recommendations instead of integrating climate-adaptation strategies within the proposed biophysical guidelines.

Explicit integration of climate-change scenarios is critical to the design and management of climate-resilient marine reserve networks. This is especially important for ecological processes such as connectivity through larval dispersal, which are essential for informing transboundary conservation. Biophysical modeling of larval dispersal is a key tool in marine conservation planning.[34,36,37] However, few models have considered the implications of climate change on multiple aspects of larval dynamics,[13,38] such as changes in dispersal distances and the availability of suitable habitats for settlement. These considerations are essential because larval dispersal across national borders may be critical for metapopulation persistence, so changes in connectivity imply changes in probability of persistence. Notably, certain areas may be less impacted by climate change and act as climate refugia,[39] providing food, shelter, and habitat, despite future changes. Identifying climate refugia at ecoregional scales is challenging and requires the use of ecosystem attributes (resistance, resilience, and persistence[40]) or environmental proxies (e.g., microclimates).[41] If we map these areas at fine spatial scales,[39,42,43] we can identify microclimate refugia for ecosystems and prioritize their protection. However, climate change may undermine the effectiveness of transboundary networks of marine reserves to facilitate recovery of exploited species. Thus, it is a priority to assess whether proposed protection targets will facilitate recovery of overexploited species in the future.

Currently, no practical guidelines exist on how to design climate-smart networks of transboundary marine reserves with explicit integration of climate-change scenarios at ecoregional scales. Given that many marine ecoregions worldwide are shared by multiple nations,[44] that climate-change impacts are currently the main threat to marine biodiversity, and that these threats are projected to escalate in the coming decades,[5] developing biophysical design guidelines and providing practical examples of how such guidelines can be developed, integrated, and harnessed could contribute significantly to climate-smart transboundary conservation.

The Southern California Bight ecoregion (henceforth "California Bight") in the northeast Pacific Ocean—shared between the state of California (USA) and the Peninsula of Baja California (Mexico)—has a long history of research cooperation.[45] It is considered a marine climate-change "hotspot"—these are rapidly warming ocean regions that are priorities for climate adaptation and represent natural laboratories for evaluating climate-adaptation options.[46] Recent marine heatwaves[47–51] and prolonged hypoxic events[18] exemplify the impacts of climate variability and environmental extremes on species, ecosystems, and coastal economies of this region. Documentation of these changes includes mass mortality events and range shifts of economically or ecologically important species.[18,47,50,52] This threatens the environmental, social, and economic sustainability outcomes that both Mexico and the United States seek to deliver through marine zoning.

In 2012, California implemented a network of MPAs covering 16% of state waters, with more than half being fully protected marine reserves.[53] However, the establishment of MPAs did not include climate-adaptation objectives.[54] Moreover, the network did not consider the transboundary nature of the region, where many species move across the United States-Mexico border. By contrast, although there are some large MPAs in Baja California, they lack integration, and less than 1% of the coastal waters are fully protected in marine reserves.[55] In 2017, researchers, fishers, governmental agencies, and non-profit organizations from Mexico and the United States co-developed biophysical design guidelines for networks of marine reserves in the Pacific region of Baja California.[55] The recommendations and guidelines are now informing the design of marine reserves in Mexico.[55]

Here we further develop and expand these guidelines,[26,27,53,55] based on a case study that specifically incorporates consideration of the effects of climate change. We propose 21 biophysical guidelines for climate-smart, transboundary marine reserve design (henceforth "climate-smart transboundary guidelines"). We focus on kelp forest ecosystems dominated by giant kelp, *Macrocystis pyrifera*, and associated focal taxa of fish and invertebrates (California sheephead, lobster, abalone, sea urchin, and sea cucumber; Table S1) to identify, analyze, and map areas that integrate and meet the proposed climate-smart transboundary guidelines for the California Bight ecoregion. Under present conditions, we quantify transboundary larval connectivity along ~800 km of coast between Mexico and the United States and project that the number of connections and the density of larvae dispersing in the network could decrease by ~50% under future climate scenarios. Population models suggest that focal taxa will generally recover if 30% of their range is protected, but future marine heatwaves could hinder subsequent recovery of vulnerable taxa in the coming 50 years. Our work suggests that ensuring that an MPA network is climate smart requires protecting critical nodes for larval dispersal and climate refugia and expanding the coverage of marine reserves. However, our aim is not to provide a comprehensive assessment of climate-change impacts in the region but rather a framework for designing climate-smart networks of transboundary marine reserves, given readily available data. We provide datasets, insights, and considerations for scientists and practitioners to use and expand on for the planning and implementation of networks of climate-smart marine reserves by 2030 in the California Bight and other ecoregions.

RESULTS

Guidelines for climate-smart and transboundary MPAs

We provide 21 climate-smart transboundary guidelines for designing networks of marine reserves (Table 1). Instead of addressing climate change and transboundary considerations separately,[26,27] we integrated both within the guidelines. Here, we provide a summary of the main recommendations (see Table 1 for more details).

We suggest that the differences in fisheries management (e.g., open-access fisheries, territorial users' right fisheries) and the level of exploitation across borders should be considered, because these differences have implications for habitat representation and the sizing of marine reserves (Table 1). We also identified the need to protect microclimate refugia to support resilience and persistence of ecosystems and the replenishment of nearby impacted areas. These refugia should be identified and defined at spatial scales fine enough to be relevant for ecosystem management.[39] Climate refugia should be identified using comprehensive proxies across the border, and, when possible, we recommend using multiple approaches to ensure the proxies are robust for multiple habitats and taxa (Table 1).

Table 1. Biophysical guidelines for the design of climate-smart transboundary networks of marine reserves and considerations for their application in the Southern California Bight

Transboundary and climate-smart biophysical guidelines	Considerations for application in the California Bight
Habitat representation and replication	
1. Represent at least 30% of each habitat type in each biogeographic subregion. Ensure representation of the variation in biodiversity across geographic gradients. Habitat representation targets should consider habitat rarity and vulnerability, and fishing pressure and management outside reserves	Habitat types include intertidal, subtidal, biogenic (e.g., kelp forests, seagrass beds), and deep-sea habitats The four biogeographic subregions include southern California, northern Baja California, central Baja California, and Guadalupe Island[85] Consider higher levels of protection for vulnerable habitats (e.g., rocky intertidal, estuaries, kelp),[5,110] rare habitats (e.g., eelgrass beds, island habitats), and overfished or poorly managed habitats[26,27] for each subregion
2. Representation targets should consider differences in fisheries management across borders[83]	California is managed through open-access fisheries while Baja California is managed through independent fishing permits and fishing concessions. For example, central Baja California has well-managed fisheries[111] that may require lesser levels of protection
3. Represent at least three examples of each habitat type in widely separated reserves to reduce the chance that they will all be impacted by a large-scale disturbance	Replicate habitats should meet a minimum size required to encompass 90% of the biodiversity associated with each habitat[53] (Table S12)
4. Represent habitats used by focal species for ecosystem resilience	Represent habitat attributes (e.g., steepness, rugosity) known to favor the biomass recovery of species[112] that enhance the resilience of ecosystems to adapt to climate change.[113] Examples include predatory species that stabilize sea urchin populations, allowing giant kelp to persist[21,113]
Protecting critical and unique areas	
5. Protect critical areas in the life history of focal species in marine reserves. Critical areas include spawning, nesting, or breeding areas, nursery habitats (e.g., estuaries and seagrass beds), and resting and feeding areas.[26,27] If necessary, combine protection with other measures such as temporal fisheries closures during spawning season or regulations to protect migratory species such as cetaceans and large sharks	
6. Coordinate binational protection and other measures when migratory species use critical or unique areas across a border	Coordinate binational protection and other measures particularly near the United States/Mexico border where there is higher cross-boundary movement (supplemental experimental procedure, Note S4, and Table S3)
7. Protect areas with special and unique biodiversity in marine reserves. Protect special and unique features including areas with remaining populations of rare species, protected species, unique habitats, healthy habitats, high species richness, and endemic species[26,27]	
8. Identify and protect microclimate-refuge habitats in each biogeographic subregion. Microclimate refugia are areas that provide refuges at small spatial scales[41,43] (few km^2) and can support the replenishment of nearby impacted habitats. These areas can be identified using environmental proxies (microclimates) or ecosystem attributes (persistence, resilience, resistance) and, when possible, using multiple approaches to ensure they are robust for many habitats and taxa	Adjust and increase representation targets for each biogeographic subregion to protect highly persistent giant kelp.[9] Protect deeper habitats used by vulnerable species (i.e., sessile species) or areas with high temperature variability, as these populations might support recovery of nearby populations after an extreme event[41,69,70]
9. Avoid identifying climate refugia at coarse resolutions that are larger than the average size of coastal marine reserves. If identifying climate refugia for specific habitats, use spatial resolutions that match the size of what is considered a replicate for that habitat	The average size of marine reserves in California is ~25 km^2, and the minimum size of coastal habitats to be considered a replicate habitat is less than 2 km of habitat along the coast (Table S12)

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Table 1. *Continued*

Transboundary and climate-smart biophysical guidelines	Considerations for application in the California Bight
Incorporating connectivity	
10. Consider movement patterns of adult and juvenile organisms when determining the size of marine reserves. They should be more than twice the size of the home range of species with short-distance movements (<10 km), and consider other management tools for species with long-distance movements (>10 km). Base the size for protection on the habitats that species use rather than the overall size of the marine reserve[26,27,60]	Ensure marine reserves extend from intertidal (minimum linear extension of 5 km) to deeper habitats (will vary depending on the slope).[53] Species movement can vary from short distances of 100 m for abalone to long distances of 100–1,000 km for sharks and tuna species[26,27,53] (supplemental experimental procedure, Note S4, and Table S3)
11. Consider transboundary larval dispersal to replenish populations within marine reserves and in adjacent areas, enhance metapopulation persistence, and support fisheries in adjacent areas. Consider larval dispersal distances for transboundary management	There is strong transboundary connectivity in the region, with larval dispersal patterns driven by seasonal north-south currents, which reverse twice a year. Marine reserves should be separated by no more than 25–100 km to ensure connectivity of species with short dispersal distances (e.g., abalone)
12. Consider large self-sustained marine reserves[56] for isolated areas to support larval self-replenishment	Species with short dispersal distances require binational coordination near the United States/Mexico border, whereas species with long dispersal distances (e.g., lobster), require coordination for the entire region Isolation can be a function of distance to nearby suitable habitat or short planktonic larval duration for certain focal species, such as abalone and giant kelp. There are isolated areas in the entire region, especially in central Baja California from 28°N to 29°N
13. Consider changes in larval duration and habitat availability due to changes in climate and ocean chemistry	Simulations suggest that a decrease in planktonic larval duration and giant kelp availability due to climate change will weaken the number and geographic scale of connections, decreasing transboundary connectivity and increasing isolation. The Channel Islands and areas in central Baja California are expected to become more isolated
14. Facilitate range shifts of species driven by climate change. Distribute reserves across geographic, latitudinal, and depth gradients to facilitate the latitudinal and depth shifts of species in response to climate change	
Allowing time for recovery	
15. Establish marine reserves for the long term (>25 years), preferably permanently, to allow populations of focal species to recover and replenish adjacent areas and maintain ecosystem functioning and resilience. When possible, establish permanent marine reserves to allow full population recovery and maximum biomass export to adjacent areas	Populations of focal species recover at different rates in marine reserves and adjacent areas in the California Bight.[78] Populations of some focal species, such as sea cucumber, are likely to recover within a decade, while others, such as abalone, will take over 40 years of protection
16. Establish permanent marine reserves near international borders	Establish permanent marine reserves near the United States/Mexico border where there is strong transboundary connectivity to maximize national conservation efforts
17. Short-term or seasonal closures should be used in addition to, rather than instead of, permanent marine reserves. Short-term (<5–10 years) closures have limited benefits for enhancing fisheries, conserving biodiversity, or building ecosystem resilience. The exception is seasonal closures that can be used to protect critical areas (e.g., spawning or nursery areas), which can be very important to protect or restore populations of focal fisheries species	
18. Assess the vulnerability and recovery rate of focal species to climate-change impacts	Sessile or low-mobility species (e.g., abalone, sea urchin, sea cucumber) are more vulnerable to climate impacts than mobile ones (California sheephead, lobster)
19. Establish permanent protection and increase the coverage of marine reserves when the objective is to protect focal species that are vulnerable to marine heatwaves	Some focal taxa that are vulnerable to marine heatwaves will likely not reach exploited equilibrium in the next 50 years (at least for populations in shallow waters), but uncertainty is high. Recovery near this level could be achieved only by permanent reserves and increases in protection. This is particularly important in Baja California, where average temperatures are higher

(*Continued on next page*)

Table 1. *Continued*

Transboundary and climate-smart biophysical guidelines	Considerations for application in the California Bight
Minimizing and avoiding local threats	
20. Establish marine reserves in areas with lower levels of cumulative threats for each biogeographic region. Consider the cumulative effects of multiple threats in each location and distinguish among threats that marine reserves cannot directly abate[114]—but can build resilience to[35]—and threats marine reserves can directly abate	While in southern California and northern Baja California areas with higher threats are mostly located near urban areas, in central Baja California and Guadalupe Island they are mostly found off the coast
21. Preferably, establish marine reserves in areas where threats can be managed effectively within reserves. Threats not directly abated by marine reserves include climate and land-based stressors. Threats directly abated by marine reserves are those related to extractive uses, such as commercial and recreational fishing and aquaculture activities	Recreational fishing is mainly concentrated near cities in southern California and northern Baja California. There is very low recreational fishing activity in central Baja California and Guadalupe Island. On the other hand, commercial fishing is located near urban areas but also in the northern Channel Islands. There is moderate fishing activity in central Baja California, mostly concentrated near Punta Eugenia

Compiled, adapted, and refined from California, Mexico, and other regions.[26,27,53,55]

We recommend considering patterns of larval dispersal across the borders and the implications for managing focal taxa with different dispersal distances. We also suggest considering how climate change will impact larval connectivity, because ocean warming could shorten the duration of larval phases, thereby limiting the dispersal capacity and the settlement of larvae to suitable habitats. For example, some places could become isolated, and large self-sustained marine reserves[56] may be needed to support larval self-replenishment (Table 1). Given the uncertainty on how species will respond to future changes, we recommend distributing marine reserves across geographic, latitudinal, and depth gradients to facilitate the latitudinal and depth shifts of species in response to climate change (Table 1).

To maximize national conservation efforts, we suggest establishing permanent marine reserves near international borders in areas frequently used by mobile species (e.g., sharks and marine mammals) and those important for dispersal of larvae (Table 1). We also recommend establishing permanent marine reserves and increasing coverage of reserves to support the recovery of focal taxa that are vulnerable to climate change (Table 1). Finally, we suggest that threats should be comprehensively mapped across borders and that decisions on the location of marine reserves should consider the threats that reserves cannot abate (e.g., climate change) but can build resilience to, as well as the threats that reserves can directly abate (e.g., fishing). The next sections describe the results of the spatial analyses used to provide recommendations for the application of the climate-smart transboundary guidelines in the California Bight (Table 1).

Habitat representation and replication: Binational mapping

Our binational habitat mapping produced spatial layers of the distribution of 31 coastal and island habitats from intertidal to deep-sea habitats for the four subregions (Figure 1 and Table S2). Although southern California covers fewer degrees of latitude than northern and central Baja California, it represents almost half (~46%) of the area of the California Bight. We found no seamounts, guyots, or other geomorphic features of importance for biodiversity in the territorial sea of the California Bight. We could not map surfgrass (intertidal and shallow subtidal seagrass) or rocky habitats deeper than 30 m for the three regions in Baja California. Finally, we found no giant kelp or estuarine habitats in Guadalupe Island.

Protecting unique areas: Identifying climate refugia

We found that kelp persistence has a positive relation with temperature variability in the three regions. The relation is significant for southern California ($p < 0.001$), northern Baja California ($p = 0.021$), and central Baja California ($p = 0.026$) (Figure 2). The slope of the correlation is similar for southern California and northern Baja California but is lower for central Baja California, which has overall higher sea-surface temperature (SST) variability. However, for SST variability values lower than 2°C,[2] the slope and positive correlation in central Baja California is like the other two regions. Our results indicate that SST variability can be used as a proxy of climate refugia for kelp forest ecosystems in the California Bight. We also recommend protecting highly persistent kelp forests as an indicator of climate refugia (Table 1).

Connectivity: Transboundary dispersal in future climates

We found strong transboundary connectivity near the United States-Mexico international border. Results of the larval dispersal models reveal that the California Current transports larvae southward throughout the year from California to Baja California, while a coastal undercurrent also transports larvae northward from Mexico toward California during summer and winter (Video S1). Under present conditions, we observed transboundary larval connectivity along a stretch of coast covering ~800 km, within which larvae from Mexico travel ~400 km north, reaching Point Conception (34.5°N) at the northern limit of the California Bight, while larvae from the United States travel ~400 km south to El Rosario (29.8°N) in northern Baja California (Figure 3A and Table 1).

For focal taxa with short planktonic larval duration (PLD), transboundary connectivity is limited because larvae of these

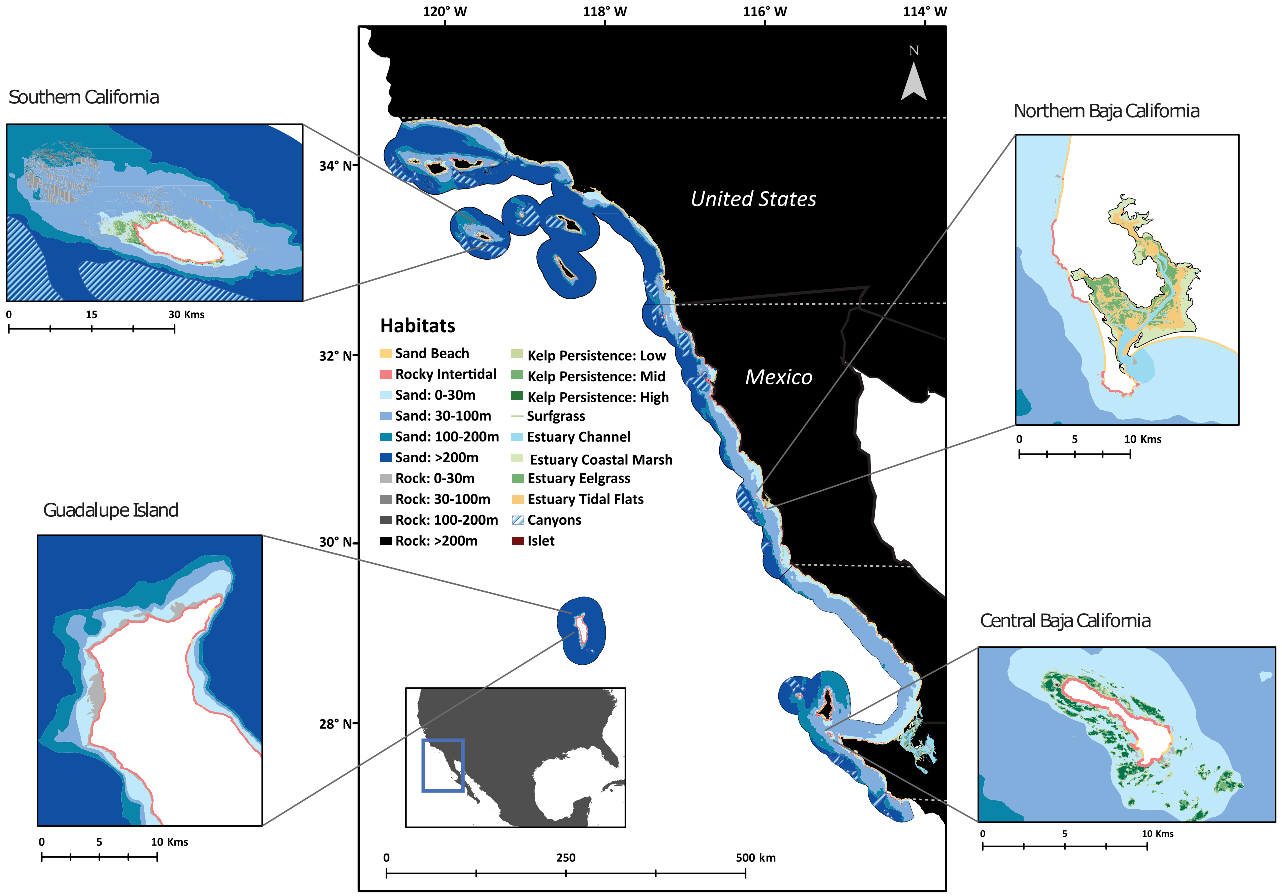


Figure 1. Distribution of marine habitats for the Southern California Bight

Insets represent examples of intertidal, subtidal, estuary, and deep-sea habitats for each subregion: Southern California for San Nicolas Island with giant kelp forests, subtidal shallow and deeper habitats, northern Baja California for San Quintín Estuary, central Baja California for Isla Natividad intertidal and shallow habitats, and Guadalupe Island for intertidal and subtidal habitats at different depths. Dashed white lines represent the limits of each subregion.

taxa move almost exclusively between adjacent sites at scales of <25–50 km (giant kelp with a PLD of a few days to hours) to 25–100 km apart (abalone with a PLD of 7 days) through the year. Focal taxa with short PLD have high levels of local larval retention (45% and 25% on average, respectively) compared to focal taxa with longer PLDs (average $\leq$7%) (Table 1). For focal taxa with short PLD, we found some isolated sites (i.e., sites with null probabilities of connectivity to other sites), such as in the offshore islands in southern California (henceforth "Channel Islands") and areas in central Baja California.

In contrast, transboundary connectivity is more important for taxa with longer PLD. Larvae of the California sheephead (PLD = 42 days) can travel 75–500 km during the fall, and larvae of sea urchins and sea cucumber (PLD = 56 days) can be transported 100–700 km during winter or year-round, respectively (Figure 3A and Table 1). The importance of transboundary connections varied by focal taxon and country. For example, for sea urchin and sea cucumber, 16%–17% of all the larvae that settled within each country originated from the other country. On the other hand, for California sheephead, 20% of all larvae in the United States came from Mexico and only 3% in Mexico from the United States. Although transboundary connectivity is more important for focal taxa with longer PLD in any single generation, long-term resilience over multiple generations depends on sites across the border that are tens to hundreds of kilometers away, even for focal taxa with short PLD.

Under a future scenario that considers the effects of climate change, the number of connections and the average density of larvae dispersing in the network decreased by about half (range from $-$24% on giant kelp to $-$63% on abalone), and the average probability of the connections was greatly reduced (range from $-$90.7% in California sheephead to $-$96.0% in giant kelp), while local retention of larvae improved for all focal taxa except giant kelp (Table S4 and Figure 3B). We found that binational connections were substantially reduced for focal taxa with long PLD (losses range 61%–27%) or lost completely for focal taxa with short PLD, either because larvae cannot reach as far or because stepping-stone connections disappeared due to the loss of giant kelp that exhibited low or intermediate persistence. For focal taxa with long PLD, the number of larvae crossing the border dropped to $\leq$3%. For focal taxa with short PLD, some sites become completely disconnected, forming independent subnetworks; other sites become only loosely connected through a few key nodes, especially around the Channel Islands and in

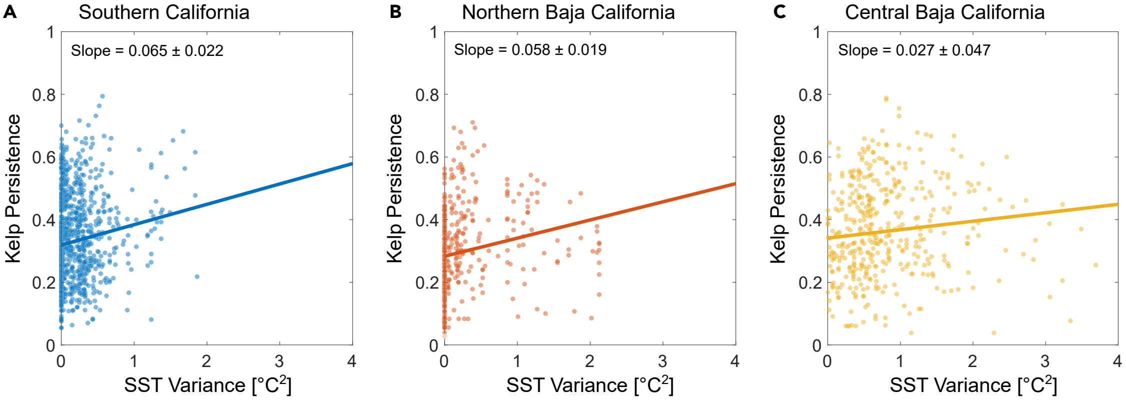


Figure 2. Sea-surface temperature variability as a proxy for microclimate refugia

Relationship between giant kelp persistence and SST variability for (A) southern California, (B) northern Baja California, and (C) central Baja California.

northern and central Baja California (Figure 3B). Importantly, under the future scenario some sites (e.g., around the northern Channel Islands and Vizcaino Bay in latitudes 28°N–29°N) are identified that may be pivotal to avoiding the collapse of connectivity in the region and which should therefore be prioritized for protection from additional impacts (Table 1).

Time for recovery: Vulnerability to climate threats

Our risk assessment indicated that mobile focal taxa are least vulnerable to acute climate stressors and that they recover the fastest because they are least sensitive to repeated disturbance. In contrast, sessile focal taxa, or species with limited mobility, exhibit high or intermediate vulnerability, and their recovery from disturbance by at least one climate stressor is slow or intermediate (Figure 4). The combination of higher vulnerability and slower recovery renders these sessile or limited-mobility benthic invertebrates most vulnerable to climate stressors (Table 1) (see Note S2 for detailed justification).

Time for recovery: Impacts of future marine heatwaves

The deterministic recovery model revealed that, overall, increased protection results in faster recovery. For all protection levels in the region (i.e., 10%, 30%, and 100%), sea cucumber showed the fastest recovery from fishing, at less than 10 years (Figure 5A). Abalone and lobster showed the slowest rates of recovery, requiring between 31 and 47 years. Importantly, our results show that protecting 10%, or even 30%, of abalone populations is not enough to reach recovery within 50 years (Figure 5A). This emphasizes the need to increase reserve coverage and to combine this with other management actions to facilitate population recoveries for slow-growing populations (Table 1). California sheephead and sea urchins showed an intermediate recovery, requiring 15–20 years, regardless of reserve coverage (Figure 5B).

In linear models of yearly density change, we found significant differences in annual relative densities of vulnerable focal taxa between years with (2014–2015) and without (1999–2013) marine heatwaves (Table S5; $p < 0.01$). Estimated annual densities of abalone, sea cucumber, and sea urchin species decreased during marine heatwaves (2014–2015) by 59.1%, 67.3%, and 72.4%, respectively.

We found an average cumulative marine heatwave intensity for 2014 and 2015 of 465.6°C days and 684.5°C days, respectively, for the pixels that overlie with the kelp forest monitoring data. When modeling future marine heatwaves for the same pixels based on regridded climate models, we project that by 2100 the probability of any given year experiencing a marine heatwave of this magnitude will be 0.46, 0.88, and 0.99 for shared socioeconomic pathway (SSP) scenarios SSP1–2.6, SSP2–4.5, and SSP5–8.5, respectively (Figure S1). Importantly, if greenhouse-gas emissions are not mitigated (SSP5–8.5), much of the California Bight could be in a permanently extreme marine heatwave within the next 50 years (Figure S1).

When accounting for potential impacts due to marine heatwaves of the magnitude experienced in 2014 and 2015 for vulnerable focal taxa, we found that no species reaches recovery status under any combination of emission scenario and reserve coverage, with abalone being particularly vulnerable (Figure 5A). While not reaching equilibrium, sea cucumbers show the largest population sizes across climate and protection scenarios. Our simulations suggest that even rapidly growing focal taxa such as sea cucumber may not reach equilibrium biomass within the next 50 years even under 100% protection (Figure 5A), but there was great uncertainty about those estimates. Together, these results suggest that levels of protection higher than 30% might be needed to support even partial recovery of vulnerable focal taxa in the face of projected increases in marine heatwave cumulative intensity (Table 1).

Minimizing and avoiding local threats: Mapping threats

We found highly threatened areas that require management to support resilience, mainly near cities in southern California and northern Baja California (e.g., Los Angeles, San Diego, Tijuana, and Ensenada; Table 1 and Figure 6A). However, in central Baja California and Guadalupe Island, we found highly threatened areas also in remote offshore sites. Both regions are isolated and scarcely populated, with Guadalupe Island located ~250 km from the mainland of the Baja California peninsula. We also found an overlap of highly threatened areas with areas of high fishing pressure in southern California and northern Baja California but also in less-populated areas in the Channel Islands and further south at San Quintín (mainly recreational

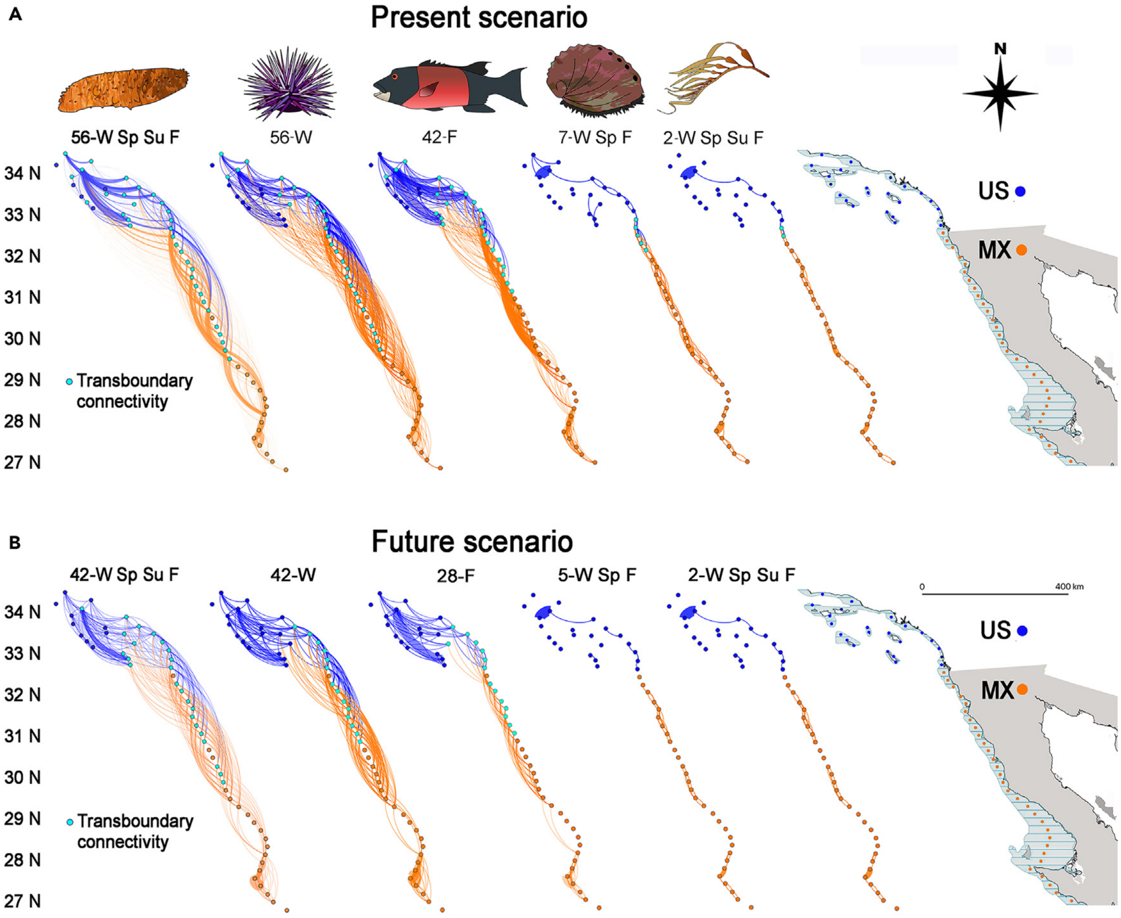


Figure 3. Networks of larval connectivity in the California Bight

Spatial networks of modeled larval dispersal for focal taxa (from left to right: sea cucumber, sea urchin, California sheephead, abalone, and giant kelp) between nodes (blue polygons are release and destination nodes delimited by the 200-m isobath). Connectivity polygons are shown on the far right. Line width represents the probability of larval dispersal (thicker lines have higher probability) and line color the country of origin. Blue-colored nodes and lines represent the United States and orange Mexico as larval origins, respectively. Sites involved in transboundary connectivity are highlighted in light blue. For each focal taxon, we indicate the planktonic larval duration (PLD, in days), followed by a letter representing the spawning season (spring = Sp, summer = Su, fall = F, winter = W; see Table S2).

(A) Present scenario, considering the PLD reported in the literature and the total area with giant kelp found within each polygon (see Figure S4 for giant kelp habitat).

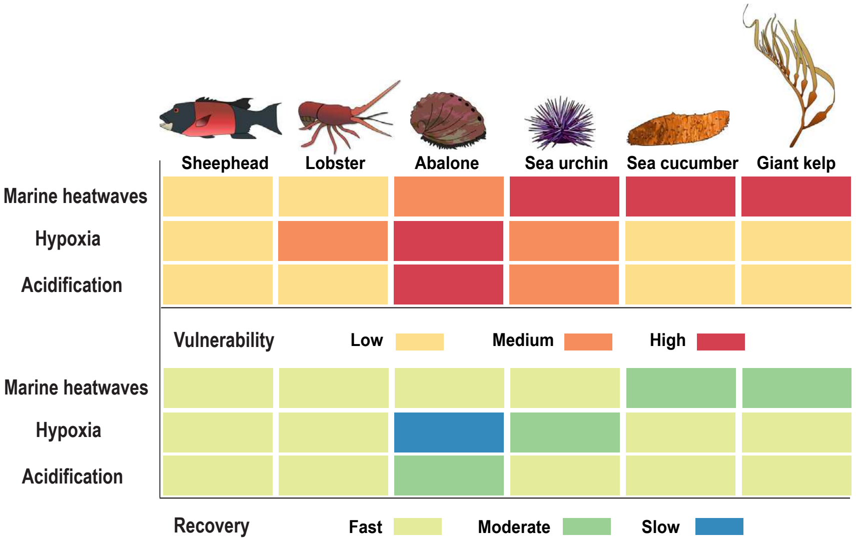
(B) Future scenario, accounting for reduction of PLD and giant kelp habitat due to climate change. Images credit: Katherine E. Dale.

fishing) and El Rosario (primarily commercial fishing) (Figures 6B and 6C). On the other hand, fishing pressure in central Baja California was lower and mainly concentrated near Punta Eugenia and Bahía Tortugas for small-scale fishing and south of Cedros Island for recreational fishing. The most important commercial fishing catches are sea urchin and lobster in southern California, sea urchin and sea cucumber in northern Baja California, lobster and abalone in central Baja California, and abalone in Isla Guadalupe (Table S6).

DISCUSSION

Our results, which consider only a selection of likely climate-change impacts, emphasize that coordinated conservation efforts for entire ecoregions will support climate-smart designs for biodiversity conservation and fisheries management to a greater degree than would networks developed separately by each nation.[34,57,58] We linked climate-smart strategies[7,10] (identifying climate refugia, incorporating connectivity, assessing vulnerability of species to climate threats, and projecting effectiveness of protection) using kelp forest ecosystems and associated focal taxa and considering future threats from climate change. Notably, the climate-smart focus of our work addresses the growing need to meet post-2020 conservation targets and protect at least 30% of the oceans by 2030 while adapting to climate change.[2]

Although southern California occupies a latitudinal distance of ~25% of the California Bight, spanning the United States-Mexico border, it contains almost half of the marine habitats and supports strong ecological connections with northern Baja California. This transboundary connectivity is already substantial for populations with long PLD and is likely to become more



	Sheephead	Lobster	Abalone	Sea urchin	Sea cucumber	Giant kelp
Marine heatwaves	🟨	🟨	🟧	🟥	🟥	🟥
Hypoxia	🟨	🟧	🟥	🟧	🟨	🟨
Acidification	🟨	🟨	🟥	🟧	🟨	🟨

Vulnerability Low 🟨 Medium 🟧 High 🟥

	Sheephead	Lobster	Abalone	Sea urchin	Sea cucumber	Giant kelp
Marine heatwaves	🟨	🟨	🟨	🟨	🟩	🟩
Hypoxia	🟨	🟨	🟦	🟩	🟨	🟨
Acidification	🟨	🟨	🟩	🟨	🟨	🟨

Recovery Fast 🟨 Moderate 🟩 Slow 🟦

Figure 4. Vulnerability of focal taxa to human threats

Ranking of focal taxa vulnerability to climate threats and their recovery rates based on scientific literature. Images credit: Katherine E. Dale.

important as species shift their distributions in response to changing environmental conditions.[5] Given that many populations of ecologically and commercially important focal taxa depend on both countries, it is essential to protect transboundary areas for larval dispersal (Table 1) to recover and maintain populations, communities, and gene flow[27,59] and benefit both conservation and fisheries.[28,34,58,60]

Our findings that transboundary connectivity is more important for focal taxa with longer PLD (Table 1) agree with empirical data on the genetic structure of these taxa. For example, while studies found strong genetic differentiation for neutral genetic markers for species with short dispersal distances, such as giant kelp[61] and pink abalone,[62] they found a lack of genetic structure for species with long dispersal distances such as California sheephead[63] and purple and red sea urchin.[64,65] To meet international commitments, California and Baja California will need to expand the coverage of protected areas. This provides an opportunity for both regions to coordinate efforts and maximize conservation and fisheries benefits based on biophysical design guidelines and modeling of larval dispersal.

Under a future climate scenario, we found that many areas become isolated and binational connections will diminish or be lost, especially for focal taxa with short PLD. However, local retention improves for most species, suggesting that establishing large marine reserves in areas that will become more isolated is critical to maintaining self-replenishment and supporting local populations (Table 1).[56] Like other studies,[13,38] we found that the strength of connections weakens, the overall larval recruitment decreases, and that some nodes for species with short PLD may become disconnected. Under a future climate scenario, networks of marine reserves will need to prioritize the protection of key stepping-stone nodes to avoid the fragmentation or collapse of larval dispersal processes in the region (Table 1).[37] If not adequately protected from fishing, depleted populations' limited supply of larvae could lead to genetic bottlenecks[62] and local population collapse,[66] with ecosystem-wide and economic implications. Without exploration of larval connectivity under future climates, these areas critical to long-term conservation efforts would not have been identified.

Our work indicates that multiple approaches are needed to identify climate refugia. We found that SST variability is a good proxy for climate refugia in the California Bight. Areas with high-frequency daily variability in ocean conditions (24 h or less) at small spatial scales provide local microclimates,[41,67,68] similarly to deeper nearby habitats where vulnerable sessile species can survive adverse conditions and mobile species can retreat.[69,70] However, we found that the relationship is weaker in central Baja California, indicating that other factors may be influencing kelp persistence. Further analyses are needed to develop robust approaches for identifying and mapping microclimate refugia for multiple taxa and ecosystems at small spatial scales (Table 1).

The probability that transboundary ecoregions will be subject to extreme marine heatwaves in the coming decades is high, and it becomes more likely every year while greenhouse-gas emissions continue to rise.[71] Even if emissions can be reduced in the coming decades, transboundary ecoregions will most likely face new extreme events. When we include the potential impacts of future marine heatwaves on the recovery of vulnerable focal taxa, our modeling results suggest that even with high levels of protection, these taxa will not fully recover in subsequent decades. Results from the published literature corroborate the notion that focal taxa with limited movement and slow recovery are more vulnerable than mobile, fast-recovering species. Increasing the level of protection and protecting climate refugia from extractive activities might be the best available climate-adaptation strategy[10] to buffer the impacts of future marine heatwaves on vulnerable species and provide a source of recovery for nearby impacted areas (Table 1).

We recommend establishing marine reserves in areas where threats can be managed effectively (Table 1). High cumulative impacts (e.g., coastal development, pollution, run-offs) are likely degrading ecosystem health, fisheries productivity, and resilience to climate change (reviewed by Green et al.[26]), preventing marine reserves from producing the expected benefits.[26,27] However, these are general recommendations, since reducing overfishing inside marine reserves, combined with other management strategies that directly address non-abatable threats by marine reserves, can build resilience,[18,19,21] thereby contributing to the recovery of degraded areas. Therefore, the decision to protect highly threatened areas requires cost-benefit analysis on a site-specific basis.[72]

It is important to note that our analyses are based on readily available data, and therefore our findings are subject to some

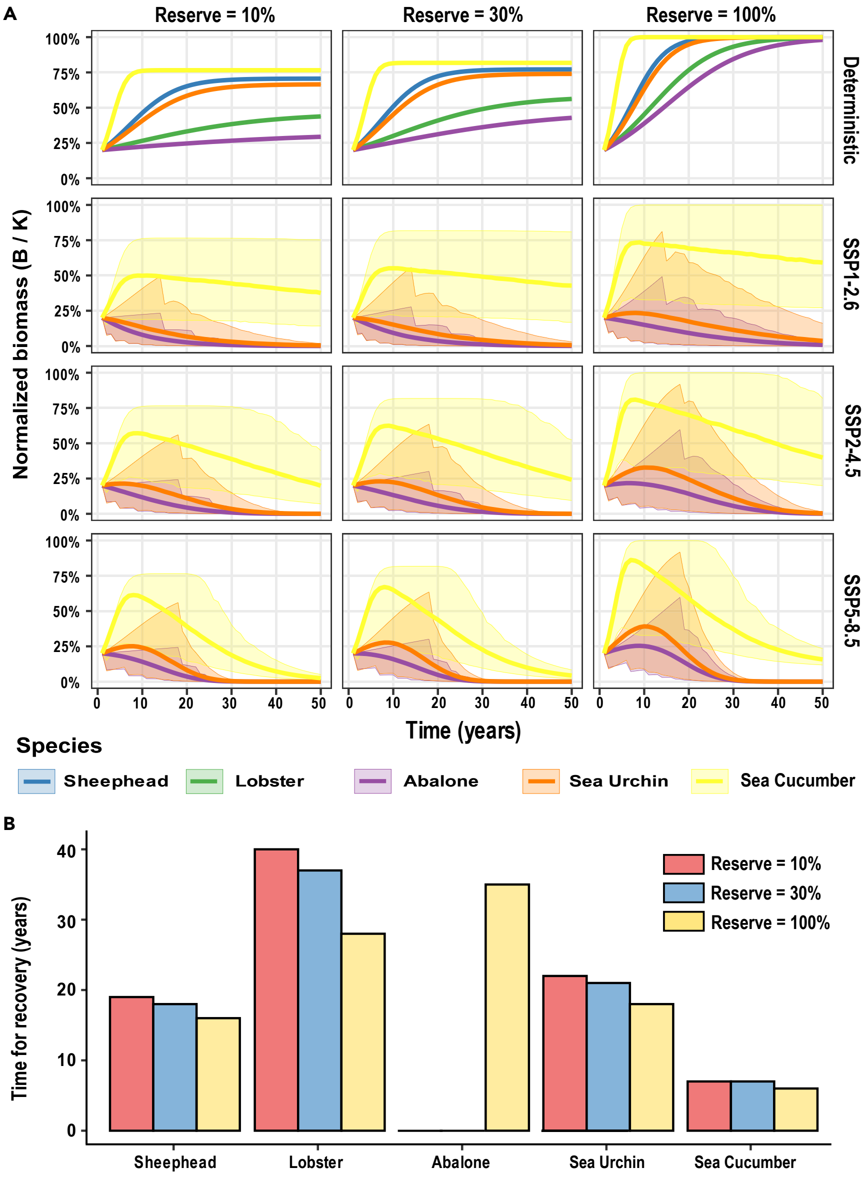


Figure 5. Simulated time to recovery for focal taxa in the California Bight under three protection scenarios

(A) Recovery pathway of five taxa (mean ± standard deviation) for scenarios of protection (10%, 30%, or 100%) under present and projected future climates. The first row of panels shows the deterministic model for all five taxa under present conditions. Rows 2–4 show results from the stochastic models for vulnerable taxa (abalone, sea urchin, sea cucumber) to marine heatwaves under three climate scenarios (SSP1–2.6, SSP2–4.5, SSP5–8.5).

(B) Time to reach 90% of equilibrium biomass for each of the five taxa across three protection scenarios under present climate conditions. Missing bars indicate no recovery within the simulated 50 years.

caveats. Although our future climate scenario provides defensible expectations of potential changes in PLD and availability of suitable habitat for settlement based on ocean warming, it does not consider effects of the potential changes in ocean circulation due to climate change or associated implications of ocean acidification. Ideally, identification of climate-smart networks of marine reserves would be based on detailed outputs from ensembles of multiple downscaled Earth system models and multiple plausible emission scenarios.[73,74] However, such ensembles simply do not exist for the California Bight because their development cost remains too high. Existing downscaled circulation models are based on only one emission scenario and three downscaled Earth system models.[75] They also do not include central Baja California.[75] Moreover, emerging evidence (e.g., Nilsen et al.[76]) suggests that the actual gains from such downscaled products do not yet warrant the effort. We therefore relied on results from an ensemble of Earth system models, which were too coarse to provide projections of detailed changes in ocean circulation but were able to provide sufficient resolution to support exploration of the indicative effects of ocean warming and intensification of marine heatwaves on focal taxa. Despite these various limitations, our findings demonstrate a subset of the plausible impacts of ocean warming on larval connectivity and impacts of and recovery from marine heatwaves. Although all estimates contain unquantified uncertainty, together they reiterate the importance of climate-smart transboundary planning.

Because it is impossible to obtain information for all habitats and species in a region, we chose giant kelp forests because of existing information on their persistence[9] and the availability of long-term information for some key associated focal taxa.[50] Moreover, kelp forests are vulnerable to the impacts of marine heatwaves globally,[48,77] acting as early indicators of climate-change impacts on other ecosystems. However, as more information becomes available, similar assessments for other vulnerable ecosystems, such as estuaries and rocky intertidal habitats, should be conducted.

Although our analyses found consistent positive correlation between SST variability and persistence of giant kelp forests for the California Bight, more research is warranted. A key issue here is that SST variability is not the only variable influencing the persistence of kelp populations or that of other focal taxa. For example, even in areas that could otherwise support persistent kelp populations, impacts from anthropogenic activities or areas with warmer waters on average might overwhelm the benefits conferred by SST variability, resulting in less-persistent kelp populations and masking any potential stronger relationship between SST variability and kelp persistence. This might explain why the strength of this relationship varies by region. For

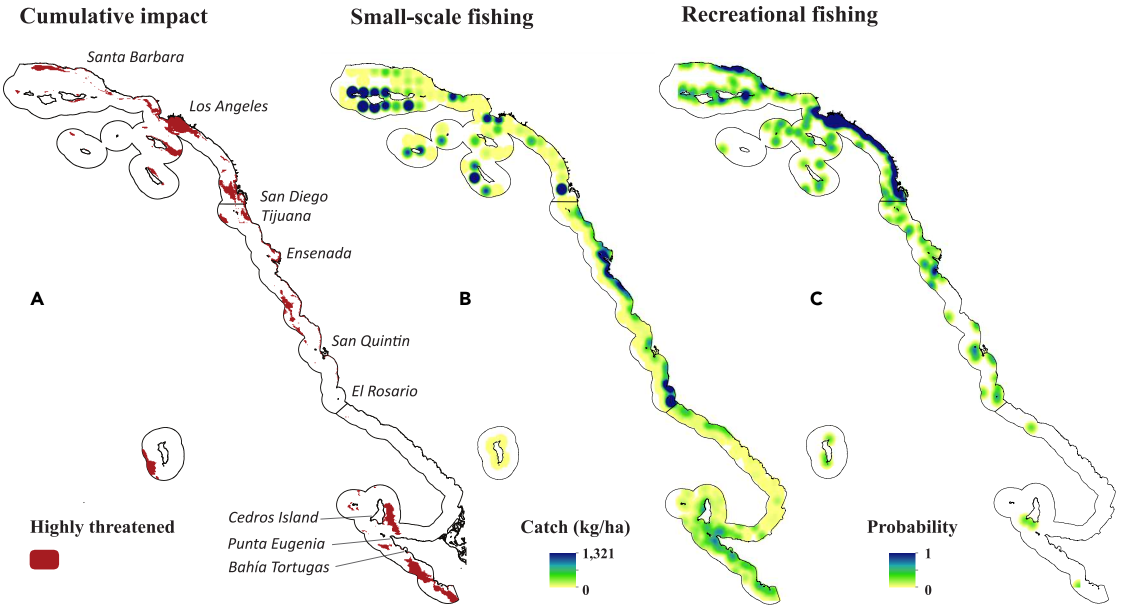


Figure 6. Distribution of threats and fishing in the California Bight

Maps of (A) highly threatened areas (top 10% of cumulative impacts of 13 threats), (B) cumulative catch for five small-scale fisheries, and (C) probability of recreational fishing in a 100-m grid square in the three regions of Baja California.

example, many of the kelp forests in mainland southern California and northern Baja California experience high levels of human impacts (e.g., run-offs, overfishing). While central Baja California is sparsely populated and its kelp forests are less impacted by human activities, they experience higher average temperatures and, thus, some populations live near their thermal tolerance limit. Robust proxies for climate refugia therefore remain elusive but also provide a focus for future research.

We also acknowledge caveats in our recovery model, which did not include the potential benefit of larval dispersal from climate refugia, where populations may be less impacted by marine heatwaves. Moreover, we based simulations of the loss of biomass on empirical data reflecting the impacts on giant kelp forests of the 2014–2015 marine heatwaves from shallower (typically <15 m) monitoring surveys.[50] We therefore urge caution in interpretation, because some deeper populations of invertebrate and sessile (or limited mobility) focal taxa might be less impacted[69,70] and may thus survive and support the replenishment of nearby affected areas. Finally, we used catch-only methods to estimate population parameters and fishing mortality. Although this might have introduced biases,[78] our parameter estimates are similar to those reported in other studies.[79] These potential limitations notwithstanding, our results reiterate conclusions of other studies that urge increased coverage of marine reserves to rebuild marine life, and they provide new insights into where such expanded coverage might provide benefits in the face of climate change.[19,80–82] Importantly, conservation is unlikely to achieve its desired outcome without other actions not included in our study, such as fishing moratoria, catch quotas, and repopulation of vulnerable focal taxa.

Fully protecting 30% of transboundary ecoregions by 2030 will require national policies, transboundary coordination, political will, and inclusive policies. As such, our proposed climate-smart transboundary guidelines will need to be combined with socio-economic and governance principles to produce effective, equitable, and robust policies and practices[55] while considering cultural and management differences across borders. Unfortunately, despite the scientific capacity and established collaboration among institutions and research groups in the United States and Mexico,[45] existing political cooperation matches neither the level of ecological connectivity observed[83] nor the needs identified under present and projected climate impacts. Urgent, coordinated binational action needs to be taken to ensure fisheries sustainability and conserve biodiversity in the region. Given the strong asymmetries in economic wellbeing, governance, implementation capacity, resources, and language, among other barriers, this goal constitutes a grand challenge, and it is a challenge that must be addressed to support the productivity and resilience of these coastal ecosystems of exceptional biological, cultural, and socio-economic importance.

Marine reserves in Baja California will require co-management that includes local fishing cooperatives complemented with other effective management strategies.[55] Some well-managed fishing concessions may need less protection and, in some cases, coordination with improved management and restoration actions may achieve biodiversity, fisheries, and climate-adaptation objectives (Table 1). On the other hand, California has the legislative infrastructure for expanding its existing network of marine reserves and the experience in marine spatial planning to create synergies across the border. This collaborative and socio-ecological setting creates a unique opportunity for the California Bight to implement transboundary and climate-smart marine spatial planning and influence marine conservation approaches worldwide.

Here, we provide a case study that links biophysical design principles for climate-smart transboundary networks of marine reserves. Our analysis suggests that achieving climate-smart status requires integrating multiple adaptation strategies such as protecting climate refugia and considering the implications of climate change for ecological connectivity and protection efficiency. Given that many marine ecoregions worldwide are shared by multiple nations,[44] our biophysical guidelines and recommendations can inform other regions' aspirations to achieve post-2020 protection targets. These regions will need to develop biophysical dispersal models to understand patterns of connectivity and identify potential climate refugia and levels of protection needed to maximize biodiversity, fisheries, and climate-adaptation outcomes. Notably, to design climate-smart transboundary networks of marine reserves, they will also need to coordinate research programs and policies while considering cultural, governance, and management differences across borders.

EXPERIMENTAL PROCEDURES

Resource availability

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Nur Arafeh-Dalmau (n.arafehdalmau@uq.net.au).

Materials availability

No new materials were generated by this work.

Data and code availability

The habitat maps and the commercial fishing and recreational fishing maps generated for this study are available in the online repository https://github.com/BajaNur/Climate-smart_MPAs. The marine habitat maps for California are available at https://wildlife.ca.gov/Conservation/Marine/GIS. The remote-sensing kelp forest dataset is available at https://portal.edirepository.org/nis/mapbrowse?packageid=knb-lter-sbc.74.13 and the codes used for the climate refugia analyses are available at https://github.com/BajaNur/Climate-smart_MPAs. The kelp forest community dataset and the codes developed for simulating the time of recovery of focal taxa are available at https://github.com/jcvdav/recovery_time. The codes developed for climate projections and marine heatwave analyses are available at https://github.com/DavidSchoeman/ArafehDalmau_MHWs. The cumulative human impact dataset is available at https://knb.ecoinformatics.org/view/doi:10.5063/F1S180FS. The small-scale fishing dataset is available on request at https://www.infomex.org.mx/gobiernofederal/home.action. https://wildlife.ca.gov/. All other data needed to evaluate the conclusions in the paper are present in the paper or its supplemental information.

Study area

The California Bight ecoregion is located in the southern California Current System in the northeast Pacific Ocean and spans the United States-Mexico international border, from Point Conception, California, USA in the north to Punta Abreojos, Baja California Sur, Mexico in the south.[44] This highly productive ecoregion, spanning over 2,700 km of coastal and island waters, is in a transitional zone between the southward-flowing, cold, nutrient-rich California Current and the northward-flowing, warm, nutrient-depleted Davidson Current.[84] It is characterized by strong latitudinal gradients in environmental conditions and oceanographic features that support a diverse assemblage of species and habitats.[84] We divided the California Bight into four subregions: southern California, northern and central Baja California, and Guadalupe Island (Figure 1). These four subregions represent geographic borders (the United States-Mexico border) and distinct biogeographic areas where species composition varies because of environmental conditions.[85]

Guidelines for climate-smart and transboundary MPAs

Our work builds on a workshop held in 2017, which developed biophysical guidelines for designing marine reserves for the Pacific region of Baja California (see Précoma-de la Mora et al.[55] for the guidelines and methods used). This involved conducting a literature review, convening multiple stakeholders (∼52 experts) from government agencies, non-profit organizations, academic institutions, and fishing organizations from Mexico, United States, and Australia to co-develop the guidelines. The group compiled, adapted, and refined the guidelines using criteria developed for California, Mexico, and other regions[26–28,53] (for more details, see Précoma-de la Mora et al.[55]). The effort was part of a series of 12 other workshops held in three priority regions in Mexico between 2015 and 2019.[55] Following the workshop in 2017, we decided to include southern California and organized a second workshop in 2019 to further develop the guidelines (following the same dynamics as in 2017, see Précoma-de la Mora et al.[55]) and expanded and refined them with a climate-smart and transboundary focus.

After the workshop, five working groups conducted spatial analyses and developed maps that integrate and meet some of the proposed climate-smart transboundary guidelines focusing on giant kelp (*Macrocystis pyrifera*) forests (henceforth "giant kelp") and five focal taxa (species or species groups) of commercial and ecological importance associated with giant kelp. We decided to focus on giant kelp forests because they are among the most productive, economically important, data-rich, and threatened ecosystems by climate change.[4,5,48] Focal taxa comprised California sheephead (*Semicossyphus pulcher*), spiny lobster (*Panulirus interruptus*), abalone (*Haliotis* spp.), sea urchins (*Mesocentrotus franciscanus* and *Strongylocentrotus purpuratus*), sea cucumbers (*Apostichopus californicus* and *Apostichopus parvimensis*), and giant kelp (*M. pyrifera*). We could not always use the same focal taxa among guidelines and analyses (Table S1) because of differences in the availability of data, and in some cases a focal taxon comprised several species.

We designed our analyses to integrate existing sources of information, develop maps, and gain insights into the impacts of future climate change to inform the application of the climate-smart transboundary guidelines for the California Bight. The working groups were coordinated and met on a regular basis for 2 years (2019–2020), and the five group leaders met on a bimonthly basis to ensure communication across groups and consistency of the analysis across guidelines. Each working group drafted their section following the same format, and the integration of the work was done in 2021 with multiple meetings, iterations, and internal revisions between the group leaders. We refined the climate-smart transboundary guidelines during the integration and further expanded the recommendations for their application for the California Bight. In the subsequent sections we describe the spatial analyses conducted to inform climate-smart and transboundary considerations for their application in the California Bight.

Habitat representation and replication: Binational mapping

We mapped the distribution of intertidal, estuarine, subtidal, and deep-sea habitats in the territorial seas (within 12 nautical miles of the coast) of the California Bight (Tables S2 and S6). We extracted depth contours (30, 100, and 200 m) from the General Bathymetric Chart of the Oceans[86] and the California Department of Fish and Wildlife (CDFW) (2010 version) using ESRI ArcGIS Pro v10.8. We then used these contours to classify subtidal habitats based on depth categories (0–30 m, 30–100 m, 100–200 m, and >200 m). We obtained intertidal, estuarine, and subtidal habitat polygons for southern California (CDFW, 2010 version) and northern Baja California from published work.[87] There was no available coastline or habitat mapping in the subregions of central Baja California and Guadalupe Island. We followed[87] and digitized the coastline and mapped intertidal and subtidal habitats for Baja California by visualizing Google Earth historical images.

We then combined existing maps of giant kelp distribution for California (CDFW, 2010 version) and Baja California[87] with a satellite time series that maps the distribution and persistence of giant kelp.[9] We characterized kelp persistence as the fraction of years occupied by kelp canopy in each 30-m^2 grid pixel for which the satellite detected kelp over the past 35 years. Pixels in which kelp was never detected were excluded from further analyses. Pixels in which kelp was detected in all years of the satellite time series were assigned a value of 1. Using these data, we classified pixels with values in the lowest quartile as having kelp with low persistence, those in the central two quartiles as mid persistence, and those in the upper quartile as high persistence. We classified giant kelp polygons that did not overlap with persistence maps as having low persistence. We also mapped the distribution of tidal flats in southern California and eelgrass (*Zostera marina*) for northern and central Baja California from existing information (Pronatura Noroeste) and *in situ* presence-absence surveys combined with low-altitude drone imagery. Finally, we cataloged geomorphic features to map submarine canyons. For more details, see Table S6). We performed all spatial analyses using ESRI ArcGIS Pro v10.8.

Protecting unique areas: Identifying climate refugia

To map climate refugia for giant kelp ecosystems, we used two existing proxies for climate variability and ecological responses: SST variability[41] and giant kelp persistence.[9] Long-term studies from *in situ* oceanographic sensors and ecological surveys empirically found that areas with high SST variability in central Baja California provide microclimate refugia for giant kelp ecosystems,[41] but it is uncertain whether such areas provide climate refugia across the California Bight. Locations with highly persistent giant kelp are a good proxy for microclimate refugia because these persistent kelp forests have endured in the past 35 years despite multiple cycles of marine climate oscillations.[9,88]

We analyzed patterns in the spatial variation and cross-correlation of these two potential indicators across a 1-km^2 grid in the California Bight. We conducted this analysis to ascertain whether SST variability can be used as a proxy of climate refugia for kelp forest ecosystems—i.e., significant positive or negative correlation between kelp persistence and SST variability—for each subregion. From the NOAA-ERDDAP data repository (https://coastwatch.pfeg.noaa.gov/erddap/index.html), we accessed 17 years (2003–2019) of daily SST data from the Aqua-MODIS satellite at 1-km^2 grid resolution. We first aggregated the 30-m^2 grid kelp persistence estimates[9] (see previous section for dataset) at a 1-km^2 grid resolution and computed their mean (values ranged from 0.03 to ~0.79). We then interpolated the SST to each grid point in the kelp persistence data using the nearest four grid points from the SST grid to construct 17-year time series for each point. We used a 30-day weighted moving average smoothing window to develop a climatology of this annual cycle. We then estimated SST variability by computing the variance relative to the annual cycle. This SST variability metric represents high-frequency (24-h or faster) temperature variability. To avoid undue influence from outliers, we used linear quantile regression of the median (using the R package *quantreg*[89]) to examine the correlation between these datasets for each subregion, excluding Guadalupe Island, which does not have giant kelp.

Connectivity: Transboundary dispersal in future climates

To assess transboundary connectivity, we implemented a hydrodynamic model, the Regional Ocean Modeling System (ROMS),[90] and calculated the average velocity fields from the ROMS, with a time step of 6 min and a saving average of 3 days (for further details of the model, see supplemental experimental procedure and Figure S2). We followed[91] and used the average current velocities from ROMS to force an offline Lagrangian module based on ROMS-AGRIF[92] version 3.0. The Lagrangian module tracks particles using a fourth-order Milne-Hamming predictor-corrector scheme. It interpolates velocities bilineally from the corners of the model grid toward the instantaneous positions, with a time step of 80 min. We then simulated the dispersal of passive spores and larvae (henceforth "larval dispersal") for five focal taxa (California sheephead, abalone, sea urchin, sea cucumber, and giant kelp; Table S1) in the California Bight. We obtained information about spawning time and PLD from the literature (Table S4) and, for simplicity, rounded to the nearest week when PLD exceeded 7 days.

To measure larval connectivity, we divided the coast into 54 polygons, each covering 20 km of latitude and limited by the 200-m isobath (Figure S3). This isobath represents the edge of the continental shelf that is a limit for coastal environments, where most fishing takes place.[44] In the centroid of each polygon, we released 1,000 virtual larvae at the start of each month of the year and followed their trajectories hourly for 60 days (2 months). We identified the intersection between each particle's location at the end of the taxon-specific PLD and each polygon using a selection-by-location function in MATLAB (Mathworks). We generated connectivity matrices reflecting the proportion of larvae that settled in each polygon relative to the total number of larvae released at each site. We averaged matrices for the larval release dates within each month during each focal taxon's spawning season. We calculated local retention as the proportion of larvae released within a polygon remaining within the natal area at the end of the PLD for each taxon. We explored connectivity matrices for each season using graph theory and a spatial network approach using the software GEPHI,[93] where nodes represent larval release sites and links represent directional larval dispersal probabilities. We estimated network density to compare changes in cohesiveness or saturation that relate to functional attributes, such as resilience.[94] We defined density as the number of links observed divided by the maximum number of possible links, representing the probability that any given link between two random nodes is present.

We simulated two contrasting scenarios to investigate the potential effect of climate change on larval connectivity due to reduction in PLD with increased temperatures and the reduction of recruitment habitat due to climate change, since both could significantly alter metapopulation dynamics.[13,38] In the first or "present" scenario, we downscaled the larval connectivity matrices to the polygon unit (following the approach described by Álvarez-Romero et al.[13]) based on two factors: probability of connections between two polygons according to the connectivity matrix based on the PLD reported for each focal taxon in the literature, and the total area with giant kelp found within each polygon.

The second or "future" scenario follows[95] a conceptual framework for assessing the likely impacts of climate change on marine connectivity due to changes in both functional and structural connectivity. For functional connectivity, we employed shortened larval dispersal distances due to warming and consequent dispersal restriction due to climate change, which relates to empirically demonstrated relationships between increases in water temperatures and changes in PLD.[96,97] For structural connectivity, we restricted the total area of available habitat to highly persistent giant kelp (Figure S4), as these kelp habitats are more likely to persist in the future than less-persistent kelp.[9,88]

We calculated the reduction in PLD (Table S4) in fish and invertebrates based on projected climate anomalies of a 2°C increase in SST. To obtain these anomalies, we bias corrected time series from an ensemble mean of 11 Coupled Model Intercomparison Project Phase 6 (CMIP6) (Table S8) Earth system models regridded to 0.25° resolution using bilinear interpolation in CDO (Climate Data Operators). Bias correction was implemented by the simple delta method (see, e.g., Schoeman et al.[74]) based on corresponding data from historical model runs and NOAA 0.25°-resolution Optimum Interpolation Sea-Surface Temperatures (OISST).[98] Anomalies were then computed as the difference between the bias-corrected SST projections over the period 2081–2100 and those over the period 1995–2014. For exploration of future marine heatwaves (see next two sections for allowing time for recovery), bias-corrected ensemble-mean time series were constructed for multiple future shared SSPs[99] used by the Intergovernmental Panel on Climate Change (IPCC). However, because in previous steps we rounded PLD to the nearest week, which effectively removes much of the contrast in results among projected SSPs, here we focused only in one scenario, SSP2–4.5, which represents an intermediate and likely mitigation scenario with radiative forcing stabilized at ~4.5 W m^{-2} by 2100.

We then used the projected temperature increase (T) under this SSP to estimate the reductions in PLD for our study region using a population-averaged exponential-quadratic model (Equation 1), based on the relationship between temperature and PLD derived by[97]

$$\ln(\mathrm{PLD}) = \beta_0 - \beta_1 * \ln\left(\frac{T}{T_c}\right) - \beta_2 * \ln\left(\frac{T}{T_c}\right)^2, \qquad \text{(Equation 1)}$$

where β_0 is 3.17, which is the value of ln(PLD) at 15°C, β_1 is -1.34, and β_2 is -0.28. Both β_1 and β_2 are parameters that adequately describe 69 species of fish and invertebrates. T_c is 15°C. For more details, see O'Connor et al..[97]

Time for recovery: Vulnerability to climate threats

Some species may be more vulnerable to climate impacts and require special measures to be implemented to promote their recovery. For this reason, we reviewed published studies of the California Bight that empirically examined the vulnerability and recovery rate of six focal taxa (California sheephead, lobster, abalone, sea urchin, sea cucumber, and giant kelp; Table S1) following marine heatwaves, hypoxia, and ocean acidification. Our search terms included "climate change," "warming," "heatwave," "temperature increase," "acidification," and "hypoxia." We defined the recovery rate as the number of years a particular focal taxon would require to recover its functional role within the system after exposure to a given stressor. For instances lacking empirical studies (e.g., effects of hypoxia or ocean acidification on California sheephead [*S. pulcher*]), we used literature from related taxa, as well as laboratory experiments, to score vulnerability and recovery rate. We scored vulnerability to climate stressors as high for lethal effects, medium for extensive sublethal effects, and low for limited sublethal effects. We scored a focal taxon recovery rate from climatic stresses as rapid (<1 year), moderate (2–5 years), or slow (>5 years). Note that the specific duration required for recovery is not available for all species (see Note S2).

Time for recovery: Impacts of future marine heatwaves

We projected the expected effectiveness of marine reserves for recovery of exploited populations, under present and projected future climates. First, we simulated the effect of marine reserves on five focal taxa within the region (California sheephead, lobster, abalone, sea urchin, and sea cucumber; Table S6), in the absence of climate-change impacts, using a deterministic, discrete-time logistic growth model with spatially implicit reserve and fishing zones:

$$X_{t+1} = X_t + \left(rX_t\left(1 - \frac{X_t}{K}\right)\right) - \left((1 - R)X_tF_{\mathrm{MSY}}\right), \qquad \text{(Equation 2)}$$

where X_t represents total biomass at time t, r is the intrinsic growth rate, and K is the carrying capacity. The last term represents harvesting of biomass outside the reserve, where the $(1 - R)$ parameterization corresponds to the portion of biomass outside the reserve. We tested three different scenarios of reserve coverage: $R = (10\%, 30\%, 100\%)$. The first two scenarios are representative of commonly cited protection targets, while the third scenario provides an upper bound of maximum attainable protection. We estimated population parameters and fishing mortality (F_{MSY}) by applying a catch-only data-limited stock assessment method[100] to catch data from 2000 to 2013 in Baja California, from Comisión Nacional de Acuacultura y Pesca (CONAPESCA) (Table S9 and Figure S5). We ran all simulations for 50 years, with initial biomass set at 20% of carrying capacity and fishing mortality outside the reserve held constant at F_{MSY}. This model has three equilibrium points. $X = 0$ implies extinction and is a trivial and unstable equilibrium. $X = K$ is a stable equilibrium point indicating that the population is at carrying capacity. An alternative stable equilibrium point is the exploited equilibrium. We considered a population "recovered" when the population size was within 90% of the exploited equilibrium ($\overline{X}$):

$$\overline{X} = \frac{K\left[r - (1 - R)F_{\mathrm{MSY}}\right]}{r}. \qquad \text{(Equation 3)}$$

For a subset of focal invertebrate taxa (abalone, sea urchin, and sea cucumber; Tables S1 and S8), we explored recovery for three climate-change scenarios by running a stochastic version of the logistic growth model. We used only these three taxa because they are highly vulnerable to marine heatwaves, while California sheephead and lobster are less vulnerable. We used the natural experiment provided by the 2014–2015 extreme marine heatwave to understand how focal species were impacted. This is the only extreme event that comprehensively impacted the California Bight and for which enough information exists to assess the response of focal taxa. We simulated the impact on the biomass of taxa based on the probability of a year experiencing marine heatwaves with a cumulative intensity at least as strong as those that impacted the California Bight in 2014–2015.[47,49,50,52] Marine heatwaves are periods where temperatures are above the 90th percentile threshold relative to a baseline climatology (seasonally varying mean over 1982–2012) and with a duration of at least 5 days.[101] We used 17 years of giant kelp forest community data (1999–2015), which integrate four different monitoring programs for the California Bight,[50] to model the rate of change of the density of the focal taxa following the 2014–2015 marine heatwaves. We excluded monitoring data north of latitude 33.8°N and west of longitude 118.7°W because this area is subject to colder average temperatures and forms a separate sub-bioregion,[102] and giant kelp forest communities there are less impacted by marine heatwaves.[103]

We selected three groups of focal taxa with limited movement that are vulnerable to marine heatwaves and estimated the change in their relative density per year at each site. We used density of focal taxon instead of biomass because size measures were not available for all sites in all years. We grouped species by genus and used five species for "abalone" and two species each for "sea urchins" and "sea cucumber" (Table S10). We scaled our density data for each focal taxon to a mean of zero and standard deviation of one per year because our data were zero-inflated and negatively skewed. We initially explored models that included the interaction effect of different levels of protection but found that protection had no significant effect on the density change in years with marine heatwaves. We then constructed linear models comparing the density change per year for each species in each site for years with (2014–2015) and without (1999–2013) marine heatwaves. We initially modeled California sheephead and lobster and found that they were not significantly impacted by the marine heatwaves and decided not to include them in the subsequent analyses. These findings are consistent with our vulnerability assessment (see results).

We used the R package *heatwaveR*[104] and the NOAA 0.25°-resolution OISST dataset[98] to estimate the average annual cumulative marine heatwave intensities (°C days) registered in 2014–2015, relative to a 30-year baseline climatology for 1983–2012. We then used corresponding daily bias-corrected ensemble means for SST from 11 CMIP6 (Table S8) Earth System models (see previous section for incorporating connectivity for detail) for three climate scenarios generated under the IPCC SSPs[99] SSP1–2.6, SSP2–4.5, and SSP5–8.5. SSP1–2.6 represents an optimistic scenario with a peak in radiative forcing at $\sim$3 W m^{-2} by 2100. SSP2–4.5 represents an intermediate mitigation scenario with radiative forcing stabilized at $\sim$4.5 W m^{-2} by 2100. SSP5–8.5 reflects an extreme climate scenario with a continued increase of greenhouse-gas emissions causing radiative forcing to reach >8.5 W m^{-2} by 2100 and rising thereafter. Using the same techniques that we deployed for the OISST data, we estimated annual cumulative marine heatwave intensities for each year for each 0.25° grid cell that overlaid with the kelp monitoring data. We then identified years between 2020 and 2100 under each of the three future climate scenarios with marine heatwaves characterized by cumulative marine heatwave intensity at least matching that registered in 2014–2015.

Using these data, we modeled the probability of occurrence of such severe marine heatwaves under each of the three future climate scenarios using a generalized linear model with a binomial link function (probability of occurrence as a function of year). Using these probabilities, we ran 10,000 independent simulations of our recovery-time model for each of the three focal taxa under each of the three climate scenarios after modifying recovery time to account for the empirically derived density change associated with the 2014–2015 marine heatwave:

$$X_{t+1} = (1 - \delta\Phi_t)\,X_t + \left(rX_t\left(1 - \frac{X_t}{K}\right)\right) - \left((1 - R)X_tF_{\mathrm{MSY}}\right), \qquad \text{(Equation 4)}$$

where $\delta \in [0, 1]$ represents the density-reducing effect of the marine heatwaves, and $\Phi_t = 1$ if the year t has marine heatwaves and $\Phi_t = 0$ otherwise. This model assumes that the growth and fishing occur before marine heatwaves impact the population. All data analyses and simulations were conducted in R 4.0.4.[105]

Minimizing and avoiding local threats: Mapping threats

We mapped climate, land-based, and ocean-based threats (Table S11) that marine reserves cannot directly abate but can build resilience to (henceforth "unabatable threats") at a 1-km^2 grid resolution in the California Bight using the most comprehensive dataset available for the cumulative human impact (see Halpern et al.[106] for dataset). We summed the value of each threat and classified those cells with high cumulative unabatable threats (top decile) for each subregion as "highly threatened." We performed the spatial analysis using ESRI ArcGIS Pro v10.8.

We mapped two extractive activities that marine reserves can directly abate: small-scale commercial fishing and recreational fishing (henceforth "fishing") in the California Bight. We mapped the total catch of small-scale fisheries (tons) for five focal taxa (California sheephead, lobster, abalone, sea urchin, and sea cucumber) (Table S6) at 1-ha grid resolution using 19 years (2000–2018) of catch information inside defined fishing blocks in California from the California Department of Fish and Wildlife and authorized fishing polygons in Baja California from CONAPESCA. In Baja California, each fishery has a designated concession or individual permit holder (hereafter "concessions") where cooperatives can extract specific resources (for more details, see Note S3).

For California, we filtered all taxon data based on data confidentiality, using only data labeled as not confidential. We estimated the centroid of each 10-min grid fishing block based on California Fisheries Chart (2001) and USCS BOEMRE imagery and georeferenced catches to the reported fishing block. Note that California closed commercial fishing of all abalone species in 1997. For Baja California, we randomized locations for catches of each focal taxon within each concession. California sheephead catch data were georeferenced assuming a higher abundance of California sheephead in the outer zones of the kelp forests, following previous approaches.[107,108] Based on catch records landing sites, we assigned each catch a random location in the outer zones of the kelp forests surrounding landing sites. We georeferenced spiny lobster catches in each authorized fishing permit or concession. Given that traps are not placed inside kelp forests nor dropped deep, we excluded areas covered by kelp and depths greater than 300 m, following published methods.[109] For abalone, sea urchin, and sea cucumber catch we georeferenced each fisheries landing using a randomizing function within each authorized fishing permit or concession delimited by diving depths between 5 and 30 m.

We then estimated the probability of recreational fishing sites in a 100-m^2 grid resolution based on georeferenced commercial and non-commercial sport fishing maps (e.g., Fish-n-Map) for the California Bight. For California, we also gathered sport fishing sites from the Bloody Decks Outdoors website (https://www.bdoutdoors.com/boating/marine-electronics/fishing-chart-southern-california/) and publicly available image maps for the California Bight. We extracted coordinates from images using "tesseract" and "magick" libraries in R. We then calculated the kernel density of recreational fishing sites using a 100-m^2 grid to assign a higher weight to areas closer to each other. For Baja California, we also consulted existing documents such as "fishing site atlas" from CONAPESCA to corroborate the geographic position of fishing sites with duplicate names or different nomenclature. These fishing documents contain latitude and longitude of all fishing sites.

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.oneear.2023.10.002.

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AUTHOR CONTRIBUTIONS

N.A.-D. and A.M.-V. conceived the study with input from F.M., J.C.V.-D., D.S.S., A.L.G., M.H.C., and H.P.P. N.A.-D., A.M.-V., F.M., A.V.-N., and J.C.V.-D. led working groups, conducted analyses, and wrote initial section drafts. M.P.-d.l.M., D.S.S., A.M.-O., K.C.C., O.S.-N., T.L.U.B., C.J.K., C.B.W., A.P.-S., and E.G.-R. led working group analyses and writing section drafts. A.A.-C., M.A., R.B.-L., M.H.C., F.C.-S., K.E.D., N.E.-A., M.W.E., J.L., A.L.F.-M., A.G.-N., A.H.-V., B.I.-M., A.F.J., L.M.-C., G.M.-M., C.O.-J., P.T.R., G.R.-O., A.R.-V., A.S., C.S., E.S., L.E.S.-R., G.T.-M., E.B.W., and S.W. supported working group analyses, data integration, and section drafting. N.A.-D., O.A.-O., N.C., S.F., A.L.G., M.G.G., B.I.-M., G.M.-M., A.M.-V., M.P.-d.l.M., H.R.-B., A.R.-V., A.S., and M.W. provided funding or supported the organization of workshops., N.A.-D. led the writing of the manuscript with the support of D.S.S. and input from all authors. All authors contributed to workshop participation and review and editing of the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

INCLUSION AND DIVERSITY

We support inclusive, diverse, and equitable conduct of research.

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