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## LETTER

## Strategically designed marine reserve networks are robust to climate change driven shifts in population connectivity

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Marine reserves can be effective conservation and fishery management tools, particularly when their design accounts for spatial population connectivity. Yet climate change is expected to significantly alter larval connectivity of many marine species, questioning whether marine reserves designed today will still be effective in the future. Here we predict how alternative marine reserve designs will affect fishery yields. We apply a range of empirically-grounded scenarios for future larval dispersal to fishery models of seven species currently managed through marine reserves in the nearshore waters in Southern California, USA. We show that networks of reserves optimized for future climate conditions differ substantially from networks designed for today's conditions. However, the benefits of redesign are modest: a set of reserves designed for current conditions commonly produces outcomes within 10% of the best redesigned network, and far outperforms haphazardly designed networks. Thus, investing in the strategic design of marine reserves networks today may pay dividends even if the networks are not modified to keep up with environmental change.

**Introduction**

Climate change is already precipitating significant changes to the world's ocean ecosystems, including shifts in species' distributions, richness, abundance, demography, and phenology (García Molinos *et al* 2015, Poloczanska *et al* 2013, 2016). These collective impacts of climate change are expected to continue into the future, altering fisheries' catch potential (Cheung *et al* 2010, Gaines *et al* 2018) and significantly impacting the future sustainability of the oceans and the social systems that rely on them (Hoegh-Guldberg and Bruno 2010, Sumaila *et al* 2011). Marine reserves are a key management tool for adapting to these climate change related challenges (Roberts *et al* 2017, Fredston-Hermann *et al*, 2018, Gattuso *et al* 2018), but it is unclear if existing reserve initiatives will meet this need, or if new reserves must be designed with a specific focus on climate change (McLeod *et al* 2009). This paper quantifies the importance of adjusting

marine reserve design to account for future climate change. In so doing, we also estimate the benefits of policy flexibility, where marine reserve designs can evolve in tandem with climate change.

Climate change raises particular questions about the effectiveness of marine reserves, which represent one of the most widespread, rapidly expanding, and globally significant tools for marine management (Roberts *et al* 2017). Under certain conditions, marine reserves can benefit both conservation and fisheries management efforts (Halpern *et al* 2010, Green *et al* 2014) and have enhanced the size and abundance of fished species inside their borders in a variety of ecosystems and geographic regions (Lester *et al* 2009, Halpern *et al* 2010, Gaines *et al* 2010). Yet the success of marine reserves depends on their spatial design; in particular, reserves are most effective at promoting fishery management when they are designed to account for connectivity (Rassweiler *et al* 2012, Gerber *et al* 2014, Coleman *et al* 2017). Other key

considerations are the size, spacing, and arrangement of marine reserves relative to scales of dispersal, species life history, and fishing behavior (McLeod *et al* 2009, Costello *et al* 2010, Rassweiler *et al* 2012). Reserves designed without this information can be ineffective or even have counterproductive effects on fishery outcomes (Rassweiler *et al* 2012). Real-world reserve design processes increasingly account for spatial information, however such strategic designs are typically based on the current biological and physical context (Hannah 2008); almost never does reserve design explicitly account for anticipated future climate change. Given the importance of accounting for the environment in reserve design, there are substantial concerns that reserves designed without accounting for climate change may have limited effectiveness in the future (Gerber *et al* 2014, Andrello *et al* 2015, Coleman *et al* 2017, Davies *et al* 2017).

Simply put, we ask whether the vast array of marine reserves around the world that were designed ‘pre-climate change’ are destined to fail in a world with significant climate change. We evaluate this possibility within a single region across seven species with a range of life history characteristics. We focus on climate-induced changes in dispersal and larval survival. As the ocean warms, larvae will generally grow and develop more rapidly, resulting in shorter larval durations, higher larval survival rates, and substantially altered spatial patterns of connectivity (O’Connor *et al* 2007, Gerber *et al* 2014). We then ask how fisheries yields will change in management contexts where reserves are fixed in place, versus those where reserves are redesigned to account for climate change. Previous work on conservation outcomes suggests that marine reserves should be redesigned to account for climate change’s effects on patterns of dispersal (Gerber *et al* 2014, Coleman *et al* 2017, Andrello *et al* 2015), but no evidence exists for the case of fisheries-focused marine reserves. Moreover, no study has yet addressed the more general question of the value of marine reserve network redesign under climate change. We investigate this question by coupling a spatial bioeconomic model, which has been used for both academic and policy purposes, with projections for how climate change will alter key parameters.

## Materials and methods

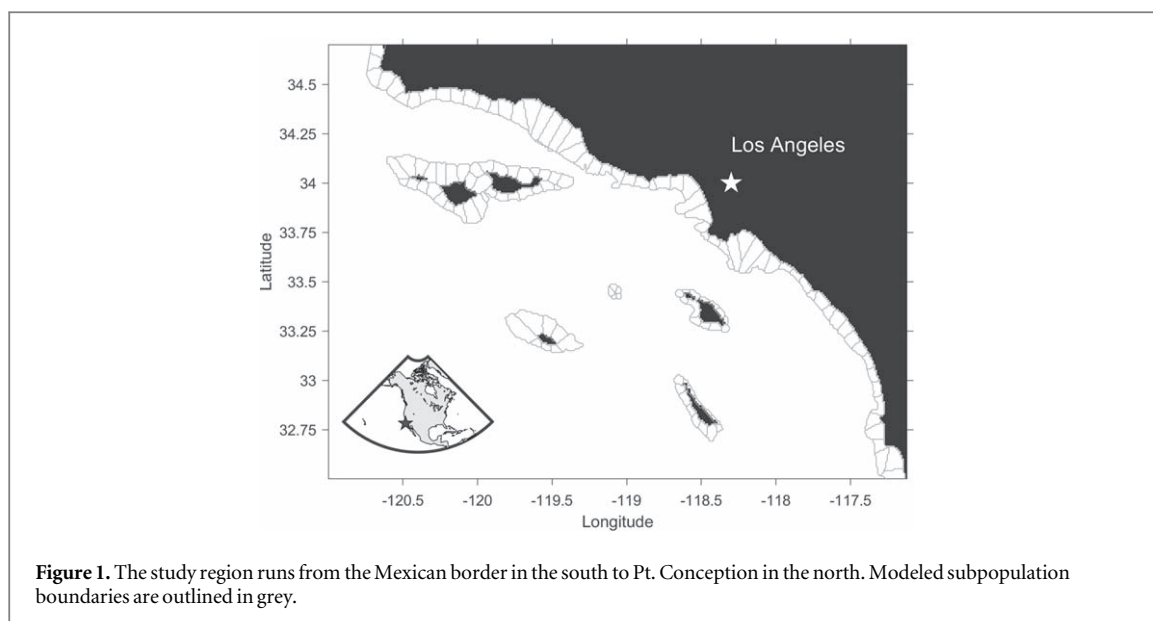
Our approach employs models and data from the southern California (USA) phase of the Marine Life Protection Act (MLPA) process. Between 2008 and 2010, a science advisory team compiled and synthesized crucial ecological, habitat, connectivity, and fishing information to evaluate stakeholder-proposed reserve designs. This resulted in the adoption of reserves that cover 16% of state waters, and the process is widely regarded as a gold standard for the design of marine reserve networks (Gleason *et al* 2010, Saarman

*et al* 2013, Sayce *et al* 2013). In this paper, we make use of the data and model structure developed in that process to compare the effectiveness of fishery-focused marine reserve networks for improving fisheries yields under today’s conditions with the expected effectiveness of those networks under projected climate change scenarios. Rather than focusing on a specific, politically agreed-upon network of reserves, we use this model and geography to explore a wide range of reserve scenarios, making comparisons between reserves optimized for fishery yield under current climate conditions and ones optimized under future conditions in which climate change has altered larval dispersal and survival.

For each of seven species targeted by fishing in Southern California, we analyze two sets of environmental conditions: current ‘pre-climate-change’ conditions and future ‘climate change’ conditions. For each species, we also explore marine reserve network designs representing four management scenarios: (1) no reserves, (2) reserves designed to maximize yields under current environmental conditions, (3) reserves designed to maximize yields under future environmental conditions, and (4) reserves that are randomly located, but that achieve a similar total area coverage to the optimized reserves in scenario 3. Optimizations are done separately for each species, and the total area covered by reserves is different for each species and scenario except for scenario 1 (no reserves) and scenario 4, in which random reserves are placed to match coverage for the same species in scenario 3. All scenarios in the main text assume overfished conditions in which fishing effort is three times the level that returns maximum sustainable yield (with no reserves) under the relevant environmental conditions. In scenarios where maximum sustainable yield is altered by changes in dispersal or survival, we thus adjust fishing effort to obtain the same relative extent of overfishing. We focus on overfished conditions as they maximize the potential value of marine reserves (Andrello *et al* 2017), but also present results for moderate fishing scenarios in the Sensitivity Analysis section of supplementary results, available online at [stacks.iop.org/ERL/15/034030/mmedia](https://stacks.iop.org/ERL/15/034030/mmedia).

## Bioeconomic model

Our bioeconomic model mirrors the model used in the Southern California MLPA process (Rassweiler *et al* 2012, Gleason *et al* 2010) but operates at a coarser spatial scale (~50 km<sup>2</sup> instead of 1 km<sup>2</sup> per management unit). We implement age-structured and spatially-explicit models of seven species that are fished commercially or recreationally and represent a range of life history and dispersal characteristics. For each species we simulate linked subpopulations in 135 patches distributed along the coast of southern California from the Mexico-US border to Point Conception and around California’s Channel Islands



(figure 1). In each patch, we model a local subpopulation of fish, in which recruitment follows a saturating Beverton-Holt function, with maximum recruitment rate proportional to the quantity of suitable habitat in that patch (calculated based on the quantity of sandy or rocky substrate down to 100 m depth). Individuals grow over time and are subjected to a constant natural mortality rate, as well as fishing mortality proportional to the fishing effort present in that location. Reproductive output from each subpopulation scales with the total biomass of reproductive-age individuals in the patch. Hyper-allometric scaling of reproduction, in which reproductive output rises faster than biomass as fish age, is not included because of limited empirical support in the species being modeled, but it is common in some fishes (Barneche *et al* 2018) and would likely increase the value of marine protected areas relative to the results presented here. Patches are linked by larval dispersal, in which the proportion of larvae produced in one patch being delivered to each other patch is based on dispersal predictions from the Regional Ocean circulation Modeling System (ROMS) simulation for the Southern California Bight (Mitarai *et al* 2009, Watson *et al* 2010, Dong *et al* 2009). The dispersal model is tailored to each species based on its pelagic larval duration (PLD) and the months during which it reproduces. Total fishing effort is held constant over time but is dynamically redistributed so that catch-per-unit-effort is the same in all patches with fishing (meaning no fisher can improve her catch by reallocating effort). We run the models long enough to obtain the yield and biomass of each species at equilibrium. See *supplementary methods: Bioeconomic model of fisheries in Southern California* and previous work for more details on the bioeconomic model (Rassweiler *et al* 2012, Costello *et al* 2010, Rassweiler *et al* 2014).

### Climate change projections

As with most marine reserve design processes, the MPA process did not formally incorporate climate change into the scientific models used to evaluate alternative marine reserve networks. Yet current evidence suggests that climate change is likely to significantly alter connectivity in this region (Hsieh *et al* 2009), and will have heterogeneous effects on species with different life-history traits. We synthesize information from climate predictions assuming an RCP8.5 scenario (the highest emissions scenario in the IPCC fifth assessment report) to estimate PLD and larval survival under future climate change (in the year 2100), using empirical relationships between temperature and PLD for marine species (O'Connor *et al* 2007).

Climate projections of Sea Surface Temperature (SST) are obtained from the Coupled Model Intercomparison Project (CMIP5) (Taylor and Doutriaux 2010) and accessed from the NOAA Climate Data Portal ([www.esrl.noaa.gov/psd/ipcc/ocn/](http://www.esrl.noaa.gov/psd/ipcc/ocn/)). We focus on RCP8.5 as it corresponds with the highest emission scenario of the Representative Concentration Pathways (RCPs) from the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC) (Pachauri *et al* 2014). We obtain SST maps for the periods 2005–2055 and 2055–2100 for the case study area (32.5–34.75 N Latitude and 121–118 W Longitude). We then calculate the average SST change for 2100, compared to the historical reference period (1956–2005). We use the average change in regional SST (2.5 °C) to predict the effect on PLD and larval survival. A sensitivity analysis of additional directions of change in dispersal is available in *Supplementary results: Sensitivity Analysis*.

### PLD and survival under climate change

Temperature has been observed to impact PLD and larval survival of marine organisms in a consistent manner across different habitats in the oceans (O'Connor *et al* 2007). We use these empirical relationships between SST, PLD and larval survival ( $S$ ) to project changes in PLD driven by climate-change-related increases in temperature, following the exponential-quadratic model in equation (1), from O'Connor *et al* (2007)

$$\ln(PLD_T) = \beta_0 + \beta_1 \ln(T/T_c) + \beta_2 (\ln(T/T_c))^2, \quad (1)$$

where  $\beta_0$  is the species-specific intercept and  $\beta_1$  and  $\beta_2$  are linear and quadratic scaling parameters which are conserved across taxa.  $T$  is the SST in the region and  $T_c$  is a reference temperature (15 °C) (O'Connor *et al* 2007). We first use this equation to calculate the  $\beta_0$  for each of our 7 species under current climatic conditions.

$$\beta_0 = \ln(PLD_T) - \widehat{\beta}_1 \ln(T/T_c) - \widehat{\beta}_2 (\ln(T/T_c))^2, \quad (2)$$

where  $T$  is the average SST for the 1965–2005 historical reference period ( $T = 18.5$  °C). We use  $\widehat{\beta}_1 = 1.34$  and  $\widehat{\beta}_2 = 0.28$  from O'Connor *et al* (2007). PLD values for our 7 species at current temperatures are obtained from Rassweiler *et al* (2012).

Once we compute the intercept values for our species at current climate conditions, we use equation (1) to calculate future PLDs for our species at  $T_{2100}$ , which corresponds to the 2.5° average temperature increase expected from climate change in the 2055–2100 period for the study area (see supplementary table 1). For example, under this increase in temperature, Kelp Rockfish PLDs will be reduced from 60 d to ~50 d.

O'Connor *et al* (2007) also predict significant increases to larval survival rates, because faster development and shorter PLDs imply less time spent in the vulnerable dispersing stage. But the effect of a shorter PLD on survival through the first year is considerably harder to predict, as any reduction of time spent dispersing will at least partially be counteracted by a corresponding increase in time exposed to post-settlement sources of mortality. In the main text we present results based on a twofold increase in larval survival, which is on the conservative end of what would be based on survival equations in O'Connor. But given the uncertainty in this process we also present results where larval survival is unchanged or even reduced by a warming ocean, to explore a broader range of possible biological outcomes (see *supplementary results: Sensitivity Analysis*).

### Marine protected area policies

We use the bioeconomic model to predict fishery yield with different MPA configurations under current and future climate conditions. We find optimal solutions with a greedy algorithm, where we randomly select a

patch and switch its management status (opening or closing it to fishing) if and only if a switch would improve overall yield. We repeat this process until yield from the resulting MPA network cannot be improved by any single-patch change. For each case we followed the optimization algorithm from 5 different starting networks; in all cases we find that the algorithm converged on the same network, suggesting that the greedy algorithm is successfully identifying globally optimal reserve networks.

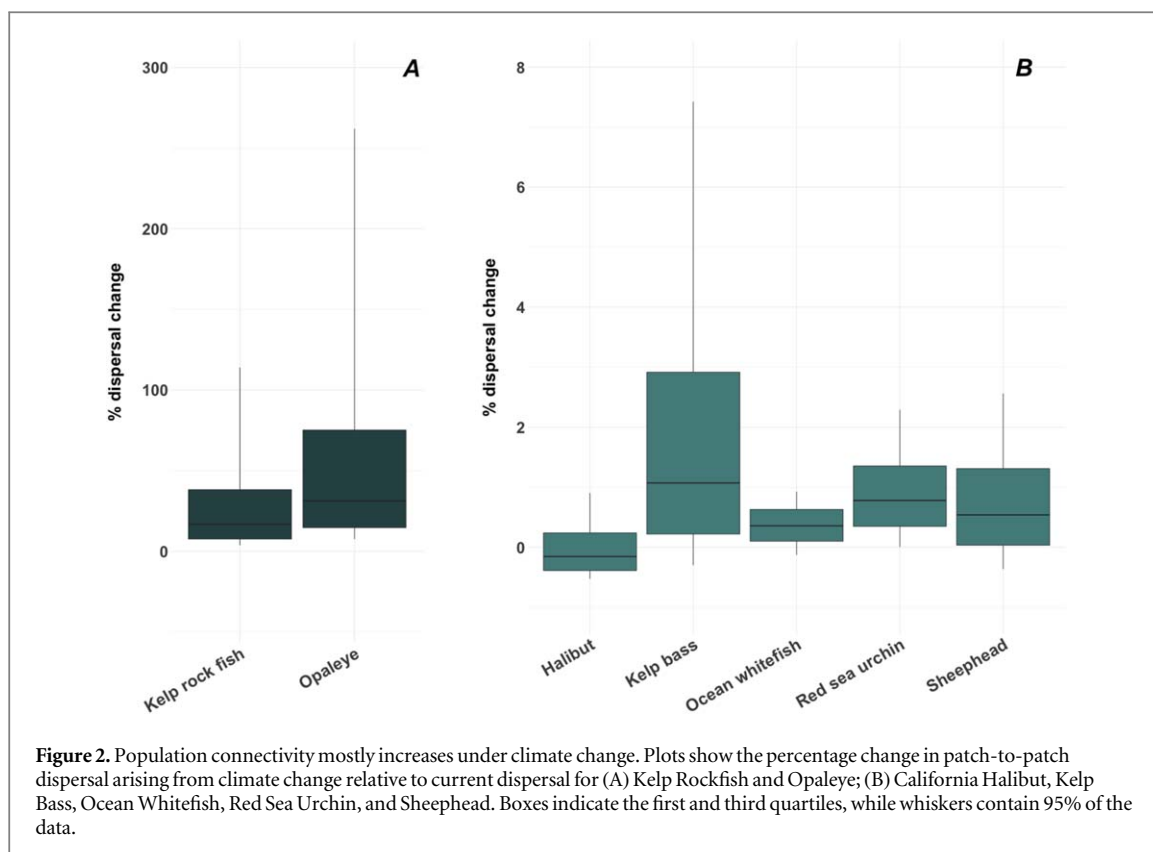
The value of an optimal MPA network is defined as the yield obtained with the optimal MPA network relative to the yield obtained without MPAs. The value of redesign is calculated as the difference between the value of the climate-redesigned optimal networks minus the value of the initial network for the same climate scenario.

We simulate random MPA networks by generating a set of completely random designs and then retaining those in which reserve coverage is within 2.5% of the coverage that gives optimal yields under the same climate scenario, i.e. in which the number of protected patches is equivalent to that in the network that has been optimized for the future scenarios  $\pm 3$  patches. The value of the random MPA network is the yield obtained from the random network relative to the yield obtained with no MPAs.

## Results

We find substantial changes in patch-to-patch connectivity arising from our climate change scenario in 2100 for the seven species we study in southern California (figure 2). For example, these data suggest that as PLD of kelp rockfish is reduced, the probability of larvae being transported from one patches to another in the region (and surviving to settlement) will increase by about 20% on average. But changes in connectivity for the species are highly variable—some dispersal pathways will decline by a few percent, others will more than double, resulting in dramatic shifts in patterns of connectivity. For all species, connectivity between nearby patches increases more than between distant patches, but shorter PLDs increase average connectivity at all scales within the study region (supplementary figure 1).

Given the well-established importance of connectivity and dispersal in optimal reserve network design, these changes suggest that marine reserve networks designed based on current environmental conditions might differ substantially from networks designed to achieve the same objective under future climate conditions. To test this conjecture, we compare networks of marine reserves that are designed to maximize total fisheries yield for each species under today's conditions with networks that are designed to maximize yield under predicted future conditions. We first evaluated whether reserve networks optimized

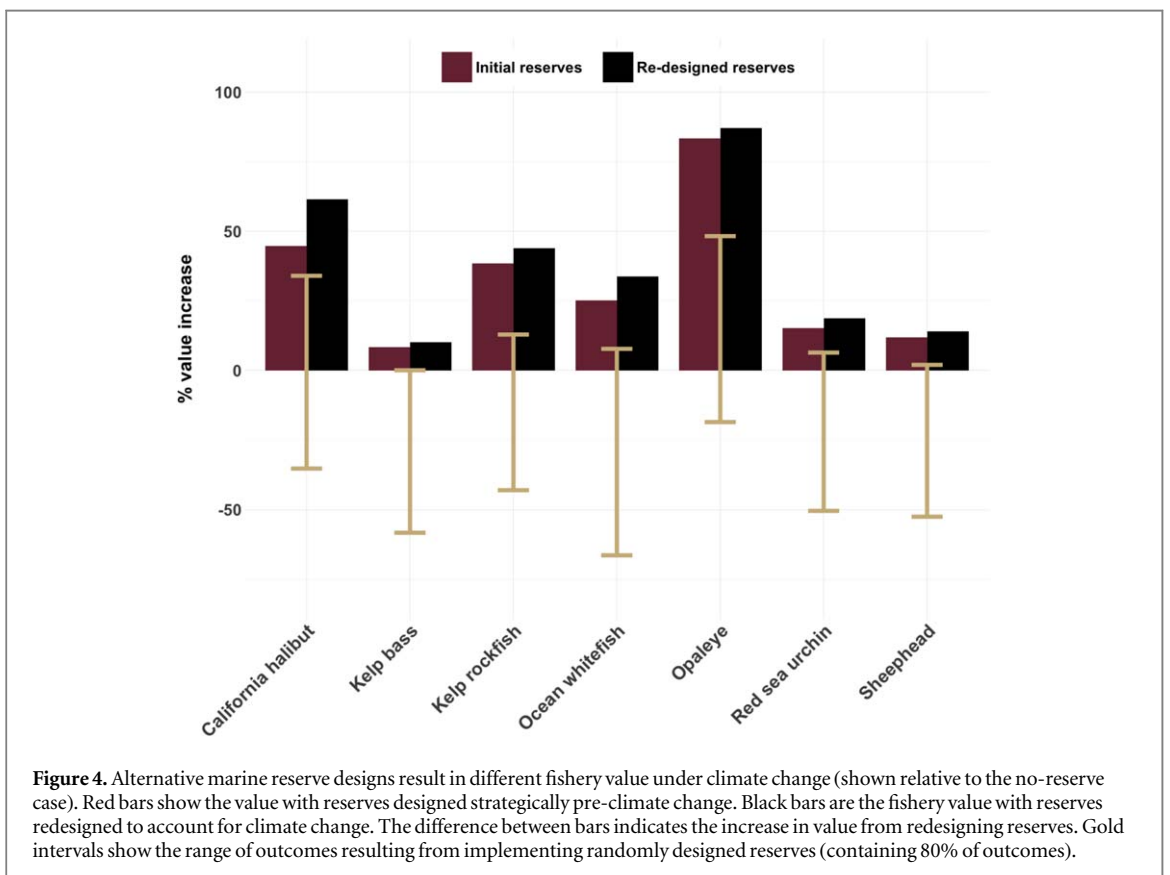
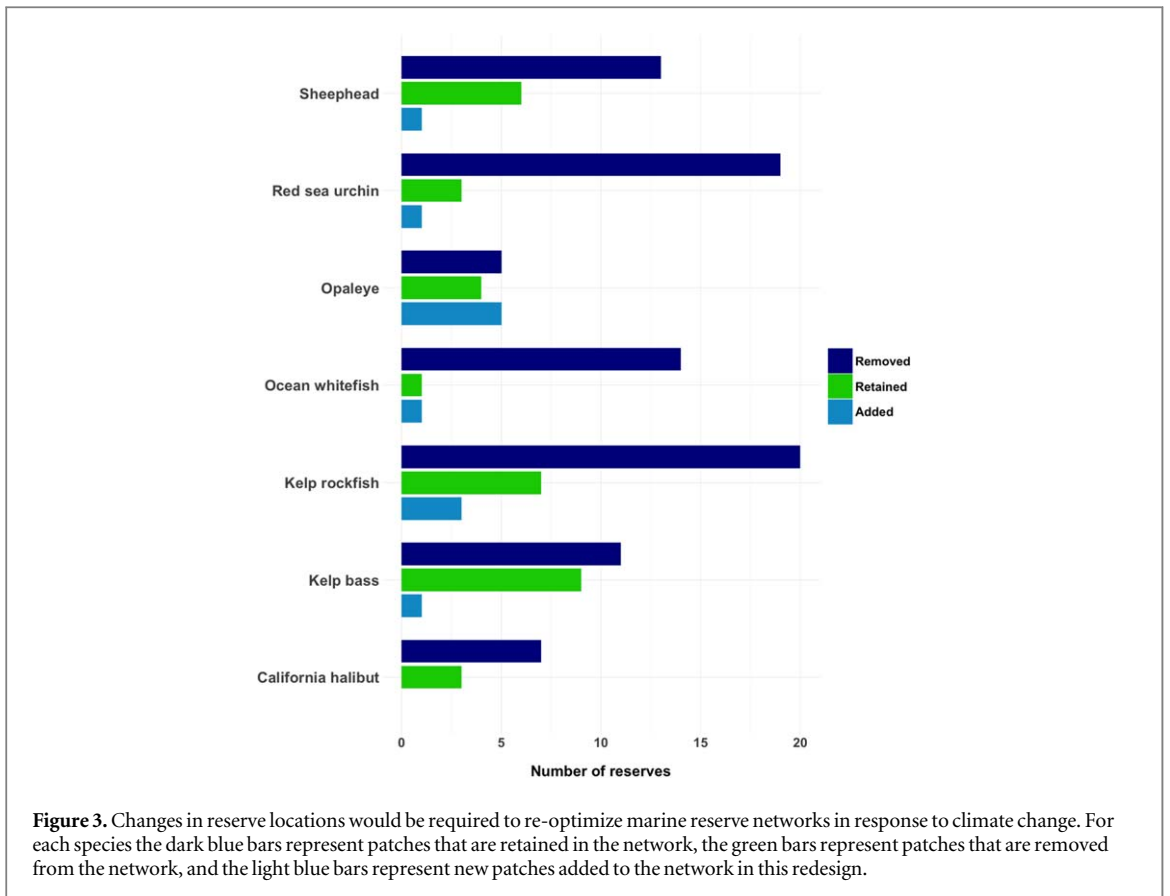


under future climate conditions differ substantially from networks optimized under today's (i.e. pre-climate-change) conditions for each species. We find that depending on the species and scenario, between 7% and 20% of the coastline should be protected under current conditions to maximize yield under overfished conditions (9–27 patches; dark circles in figure 3; for moderately fished scenarios see *supplementary results: Sensitivity Analysis*). For all species considered, many patches optimally protected under today's conditions are not included in the optimal future network (55%–93% of today's patches are removed; green bars in figure 3), and for all but one species, some patches that would be open to fishing in an optimized network today should be closed under future climate change (5%–56% of patches in optimal future networks are new; light blue bars in figure 3). For example, if a currently optimal network for sheephead is redesigned under climate change, 13 patches would be deleted from the reserve network, 6 patches would remain the same, and one new patch would be added. These results show that re-optimizing marine reserves in response to climate change would entail substantial alteration of the initial spatial plan.

But these results say nothing about the value or importance of redesigning the network. Put differently, if we adhere to the initial design, developed without accounting for climate change, how well will it perform under predicted future climate change? To explore this question, we compare the fishery yield from the initial (pre-climate change) network to the fishery yield from the redesigned (with climate

change) network, asking how each network will perform under future climate change conditions. Although the redesigned reserve network necessarily performs as well or better for every species, the degree of improvement over the initial reserve design is often surprisingly small. Figure 4 illustrates the increase in sustained fishery yield that is expected from each marine reserve network relative to a system with no reserves. The value of optimally designed reserves under climate change is indeed substantial for most species, with the redesigned reserves increasing yields between 5% and 90% (light blue bars) relative to a situation with no reserves. Yet we find that much of this value is also captured by the initial reserve design (4%–85% increase over no reserves, dark blue bars). For example, kelp rockfish yields are about 40% higher with the initial set of marine reserves than with no reserves. The yield for this species can be further increased by optimally redesigning marine reserves, but only by about 5 additional percentage points. These results illustrate that a strategically designed network of marine reserves, optimized under current conditions, is likely to continue to perform well in the future even as the climate changes.

Does this finding imply that marine reserves will perform well regardless of where they are placed? To address this question we generate 14 000 randomly designed marine reserve networks, each with a total protected area that is similar to the area of the reserve network that gives the greatest sustainable fisheries yield for that species (within 2.5% of the total area protected by the optimal network). While marine reserves



are probably never randomly placed in practice, this comparison allows us to separate the expected effect of a given level of marine reserve coverage from the effects of reserve placement. Randomly placed reserves perform much worse than strategically designed ones, and in most cases actually reduce fisheries' yields (gold intervals, figure 4). These results underscore the value of strategic design, and confirm that the improvements in outcomes promised by such designs are likely to be robust to anticipated changes in environmental conditions.

## Discussion

Climate-induced reductions in PLD and larval survival will result in substantial changes in realized population connectivity and in the optimal placement of marine reserves. However, perhaps more importantly, we find that relocation of marine reserves brings only modest benefits over currently optimal marine reserve networks. The approach we take is generous to the potential value of redesign under climate change in the following ways: we use a relatively extreme future climate change scenario; we focus on an overfished state in which marine reserves are especially valuable; we look over an undiscounted horizon in fixed future conditions, which maximizes the potential to tailor redesign for those conditions; and we focus on individual species, which allows marine reserves to be tailored to each species, thus maximizing potential value. Our overall qualitative results are robust to a range of fishing and climate scenarios (see *supplementary results: Sensitivity Analysis* and supplementary figures 2–5). For example, the benefits of reserve redesign are quite low when fisheries are well-managed outside (i.e. fishing pressure is set to a level that maximizes yields in the absence of marine reserves). We do not examine the scenario in which a reserve design process incorporates climate change projections in the initial choice of locations, placing fixed reserves optimized to perform well under current conditions and under expected changes to dispersal. It seems likely that designs that anticipate climate change will outperform designs that neglect it, but the magnitude of this benefit will depend on the accuracy of our climate projections, the pace of change, and the relative value we place on current and future yields.

Here we explore changes in larval connectivity and larval survival because they are key factors influencing the optimal location of marine reserves, and because we have quantitative, empirically grounded predictions of how they will change as temperatures rise (Costello *et al* 2010, Andreollo *et al* 2017). But a range of other biotic and abiotic factors are likely to be altered by climate change, and important questions remain about how these factors will jointly affect population dynamics and management. For example, ocean productivity and ocean currents are likely to change in

spatially complex ways in the future, but we lack fine-scale predictions of these changes so they are difficult to incorporate into models of future conditions. Extreme events such as marine heatwaves are also expected to increase in frequency and magnitude causing species mortality (Smale *et al* 2019). Similarly, ocean acidification associated with climate change may alter larval behavior (Munday *et al* 2009), growth and survival (Baumann *et al* 2012) with complex effects on population connectivity and dynamics.

Overall, these findings suggest that while redesigning marine reserves to explicitly account for climate change effects on dispersal can confer some additional benefits for fisheries yield, those benefits may be quite modest. This general conclusion holds across a wide range of species life history and climate change effects, suggesting existing reserves that are optimally designed for today's conditions are likely to continue to perform well, even in a future with significant climate change.

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## Data availability statement

The data that support the findings of this study are available from the corresponding author upon request.

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