

# Assessing the Population-level Conservation Effects of Marine Protected Areas

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## Abstract

Marine Protected Areas (MPAs) cover 3-7% of the world's ocean, up from less than 1% in the year 2000, and international commitments call for 10%, 30%, and even 50% coverage. The premise underlying MPA expansion is that they conserve biodiversity, habitats, and fished populations. While numerous studies show that MPAs produce conservation benefits *inside* their borders, many MPAs are also justified on the grounds that they confer conservation benefits to the broader population *beyond* their borders. This paper examines the conditions under which MPAs can provide population-level conservation benefits inside and outside their borders, and shows that even in cases when the conservation benefits are large, they are inherently difficult to detect empirically. A network of MPAs was put in place in The Channel Islands National Marine Sanctuary in 2003, with a goal of providing regional conservation and fishery benefits. Evidence indicates that the Channel Island MPAs have increased biomass densities inside the MPAs, but we are unable to find a clear effect of these same MPAs at the population level. MPA effect sizes less than 30% are likely to be difficult to detect (even when they are present), and the size of many MPA networks suggests that effect sizes may often be smaller than 30%. Our results provide a novel assessment of the population-wide effects of a large and iconic Marine Protected Area network, and provide guidance for communities charged with monitoring and adapting MPAs.

# 1 Front Matter

## 1.1 author\_contributions:

D.O., S.G., and R.H. developed structure of simulation model. D.O., O.D., C.C., and J.C. developed estimation strategy. J.C. provided support on collecting and interpreting data. All simulations, statistics, and sensitivity analyses performed by D.O. and O.L. . All authors contributed to the manuscript.

## 1.2 conflict\_of\_interest:

R.H's research program receives funding from environmental NGOs, foundations, fishing industry, governments and international agencies. All of these can be interpreted as a conflict of interest when evaluating fisheries policy. C.C., S.G., and O.D's research program includes funding from environmental NGOs and foundations with an interest in ocean conservation and food security. ## significance Healthy marine ecosystems are critical to the well-being of the planet. Marine protected areas (MPAs) are increasingly being used to conserve and manage these ecosystems. Our study pairs theory with empirical methods to show that the population-level conservation effects of marine protected areas can be highly variable and dependent on human drivers. We find no statistically clear effect of a large and well protected network of MPAs in the Channel Island, California, on targeted finfish after 14 years of protection, which our simulation analysis suggests is actually to be expected. MPA practitioners must clearly communicate expectations from MPA networks, and plan monitoring and adaptations strategies that directly address the challenges of estimating population-level conservation effects of protected areas.

## 1.3 acknowledgements

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## 1.4 keywords:

- Marine Protected Area Networks
- Conservation
- Bio-economic modeling
- Program Evaluation

## 2 Body

No-take Marine Protected Areas (MPAs), spatial regions of the ocean in which fishing is prohibited, have a long history in the management of marine resources. Traditional cultures in Oceania utilized - often temporary - MPAs as “fish banks” for times of need (1). Modern MPAs were first established primarily as marine analogs to the terrestrial protection of iconic landscapes like Yellowstone or Kruger National Parks (2, 3). Over time our goals and expectations for MPAs have evolved; while all MPAs are expected to deliver conservation benefits within their borders, many modern MPAs are also established to bolster fish populations throughout the region in which they are located (4).

Recent international agreements to expand MPAs (most proximately, the Convention on Biological Diversity’s Strategic Plan for Biodiversity, which calls for 10% of coastal waters to be protected inside MPAs by 2020 and the International Union for Conservation of Nature call for 30% by 2030) are based on the expectation that well-designed MPAs will achieve benefits both within, and outside, their borders. Numerous studies provide evidence that well-enforced and appropriately sized MPAs can produce conservation benefits within their borders (5–8). However, our collective scientific understanding of the regional-scale impacts of current and future MPAs on fish populations and fisheries is surprisingly limited.

As conservation benefits accrue inside MPAs, theory holds that MPAs can affect the waters beyond their borders through the spillover of adult and larval fish from the protected to the fished areas, as well as through displacement of fishing effort. These dynamics link fish both inside and outside of MPAs as part of a shared biological stock; the population. Several studies have documented empirical evidence for the existence of adult or larval spillover affecting both abundance and fisheries (9–17), as well as alteration of fishing effort in reaction to (18–20) and in anticipation of (21) MPA placement. However, empirically detecting the net effects of spillover on entire fish populations and fisheries is much more difficult. From a fishery perspective, are spillover benefits sufficient to offset losses in fishing grounds and changes in responses of displaced fishers caused by an MPA? From a conservation perspective, how much does the buildup of fish inside an MPA

77 increase biomass outside the protected area? Overall, what are the population-level effects of MPAs?

78 As stakeholders around the world seek to use MPAs in marine resource management portfolios, it is critical  
79 that we develop a better understanding of the magnitude and drivers of population-level MPA effects. This is  
80 particularly true in the context of a changing climate, in which “set it and forget it” management strategies  
81 are increasingly untenable; we need to be able to monitor the performance of MPAs in order to adapt them  
82 as dictated by a shifting environment. The MPAs within the Channel Islands National Marine Sanctuary,  
83 California, USA (hereafter the Channel Islands) provide an ideal case study to address this need. A network  
84 of protected areas covering approximately 20% of the Islands’ waters was put in place in 2003 (22). This MPA  
85 network has subsequently been used as a model case study in protected area design around the world (24).

86 We use data from the first 14 years of protection to provide what is to our knowledge the first empirical  
87 assessment of the population-level effect of a large MPA network on a wide array of finfish species. In contrast  
88 to clear differences in biomass densities observed inside and outside of well protected MPAs both globally (5)  
89 and in the Channel Islands (26) we are unable to detect a clear population effect from the Channel Islands  
90 MPAs. We build off of existing MPA theory to consider why this might be, and provide guidance for scientists  
91 and managers as to when and how we might expect to estimate the population-level conservation effects of  
92 MPAs.

## 93 **2.1 Results & Discussion**

### 94 **What Are the Population-Level Effects of MPAs?**

95 The empirical MPA literature has generally focused on assessing conservation effects within the borders  
96 of protected areas (7). While these within-MPA effects are vitally important for protecting rare species,  
97 biodiversity, critical habitats, and often tourism, they paint an incomplete picture of the overall population  
98 effects of MPAs. The organisms within the borders of protected areas are generally part of a broader  
99 biological stock, connected through adult movement and larval dispersal. The assumption that MPAs will  
100 have conservation benefits beyond their borders for most species is implicit in all multilateral calls for MPA  
101 expansion, but these benefits have not been widely measured.

102 We define the population-level conservation effects of MPAs as the change in mean total biomass densities of  
103 targeted finfish both inside and outside of MPAs, relative to the mean total biomass densities of targeted finfish  
104 inside and outside of MPAs that would have occurred without the MPAs. As an example of a population-level  
105 MPA effect, consider a evenly distributed population that has 50% of its range protected by an MPA. Suppose

that the MPA increase biomass densities inside the reserves by 20%, and by 0% outside the reserve. By our metric the population conservation effect of the MPA would be 10%.

Numerous factors can affect the population effects of MPAs. These include the scale of adult and larval dispersal relative to the size of the MPAs (8, 27–30), larval dispersal patterns and the strength and timing of density dependence in the population (e.g. pre- or post-settlement, (31)), the age and degree of enforcement (7), how overfished the population would be without the MPA, and how fishing and management responds to the implementation of the MPAs (4, 32–43). In addition, even for the same total area of MPAs, the location and spacing of the MPAs can have a profound influence on their cumulative impact through network effects (4, 44).

Given this existing body of theory, what should we expect *a priori* the effect size of the Channel Islands MPAs to be? While we know many parameters will affect the expected effects of the MPAs, theory suggests that life history, adult and larval dispersal relative to MPA size, and fishing pressure will be key drivers. The targeted species in our database span a range of life histories, but are largely made up of fishes in the perch and rockfish complexes, with a mean Von Bertalanffy growth coefficient of 0.32, and a mean age at maturity of 4 years (45).

The MPAs in this study cover 20% of the surface waters of the Channel Islands, a region spanning roughly 90km east to west. Detailed dispersal studies are not available for all of the species covered by our study, but what information we have suggest that while adults of some of these species are likely to exhibit site fidelity (46), larvae are likely distributed beyond the Channel Islands (47). Therefore, if we assume that the population of the targeted species is at least equal to the extent of the Channel Islands, we can assume that at most the MPAs cover roughly 20% of the targeted populations' ranges.

Formal stock assessments are largely lacking for these species. However, what evidence we have suggests mostly moderate fishing pressure, with some species such as California sheephead (*Semicossyphus pulcher*) and blue rockfish (*Sebastes mystinus*) experiencing high levels of fishing mortality, likely resulting in biomass levels below management targets during the early 2000s (48, 49).

We integrated these network design features, life history traits, and exploitation histories into a spatially explicit bio-economic simulation model, and used this model to generate expected outcomes for the Channel Islands MPAs, varying key unknowns such as the degree of pre-MPA depletion, species' movement rates, and fleet dynamics. While a wide range of MPA effects are plausible, from 0% to upwards of 200%, the median simulated effect size for a stylized version of the Channel Islands after over ten years of protection was roughly 16% (Fig.2).

### 2.1.1 Effects of the Channel Islands MPA Network

Having established a theoretical grounding for the likely biomass density outcomes of the Channel Island MPAs, what empirical evidence do we have of the effects? (26) examined changes in biomass densities of species targeted by fishing activity inside and outside of the MPAs over time (a metric generally termed a “response ratio”), and compared these changes to the trends in non-targeted species. They found a statistically significant increase in the response ratios of targeted species over time, and evidence that this increase is smaller in the non-targeted species. Updating the results of (26) through 2017 with a Bayesian response-ratio regression shows a continuation of the increasing trend in the response ratios of targeted species (Fig.1). This provides evidence that the Channel Islands MPAs are large enough and sufficiently well-enforced as to provide meaningful protection within their borders.

Unfortunately, these response ratios do not provide sufficient evidence for significant population-level effects of the Channel Islands MPAs. Control sites used in calculating response ratios are often selected based on abiotic or ecological traits such as habitat characteristics (50). Selection of these sites is complicated, though, by the very spillover that MPAs are often intended to create. Export of adults or larvae from the MPA to the “control” site affects their status as controls, as does displacement of fishing effort from MPAs to control sites. In theory, control sites far enough away to negate both biological spillover and concentration by the fishing fleet could be selected, but finding suitably far sites that are also appropriate proxies for the ecological and economic context of the MPAs may be challenging. As a result of these challenges, response ratios can be a highly imprecise and biased measure of the population-level conservation effect of an MPA network (50).

In the case of the Channel Islands MPAs, control sites are often located within a few kilometers of an MPA, suggesting that they are susceptible to both local biological spillover and by concentration of fishing effort excluded from the MPAs. Given these complications, we can interpret the response ratios reported in (26), and updated here, as evidence that the MPAs are providing effective protection of targeted fish biomass inside their borders, particularly in light of the general increase in response ratios over time. But, we cannot use these response ratio results serve as a definitive indicator of overall population effects of the MPAs.

To illustrate this problem, we simulated response ratio trajectories for species and MPA coverage representative of the Channel Islands (see methods and SI for details of model structure). These simulations cover the life-histories and MPA sizes seen in the Channel Islands, but vary in key unknowns such as the actual degree of fishing pressure, the timing of density dependence, and the fishing fleets response to the MPAs. For each year of protection, we paired our simulated response ratios to the estimated posterior probability distributions of the empirical Channel Island response ratios. For example, if the mean estimated response ratio in the year

2006 (year three after implementation) is one, we found all simulations that had simulated response ratios near one after three years of protection, and then pulled out the “true” simulated population-level MPA effect from each of those simulations. This provides us with a distribution of simulated population-level MPA effects that could plausibly generate the types of response ratios actually observed in the Channel Islands.

The response ratio trends we observe in the data could plausibly be produced by a wide range of population-level MPA effects (Fig.1). Response ratios well over one were associated with population-level MPA effects generally less than 25%, and, importantly, many simulations produced large response ratios but population-level MPA effects close to 0%. This can occur if for example fishing pressure is only moderate, adult movement is low, larval dispersal is high, and displaced fishing effort concentrates around the border of the MPAs.

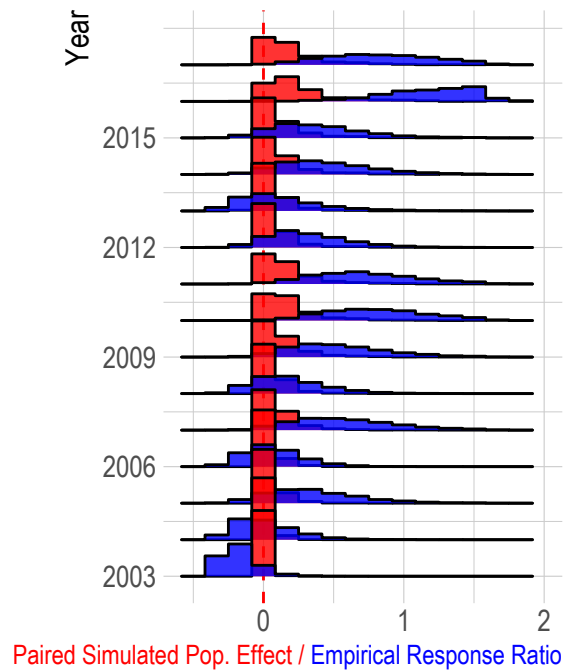


Figure 1: 90% Posterior probability distributions of response ratios for targeted species (x-axis) over time (y-axis) in blue. Simulated population-level (pop.) effect on biomass densities matched to empirical response ratios in red. For response ratios, a value of zero indicates that biomass densities of targeted species are identical inside and outside MPAs, a value of one that biomass densities of targeted species are 100% inside MPAs relative to outside. For MPA population effect, a value of zero indicates that biomass densities are identical in the with- and without- MPA scenarios. A value of 1 indicates that biomass densities are 100% greater in the scenario with MPAs than the scenario without MPAs.

Given the potential unreliability of response ratios for the task, how can we empirically measure the population-level effects of MPAs? The perfect experiment would involve two parallel worlds that were identical, except

for the implementation of an MPA. In world “A”, no MPA would be implemented, and in the facsimile world “B”, the MPA would be implemented. Both worlds would be tracked before and after MPA implementation, and the biomass densities would be compared after treatment. Instead of two parallel worlds, a similar experimental design would involve random placement of MPAs. Unfortunately, neither of these experimental designs has been implemented, because parallel worlds do not exist and MPAs are to our knowledge never placed at random. Careful causal inference requires some other means of controlling for biases introduced by factors such as the unobserved environmental shocks, the MPA siting process, biological spillover, and concentration of fishing effort (50, 51).

Building off of the concepts explored in (26), we used an identification strategy utilizing biomass densities of 11 species that are not directly targeted by fishing before and after MPA implementation as our control group (non-targeted), and biomass densities before and after MPA implementation of 12 species targeted by fishing as our treatment group. Targeted species in the Channel Islands, include commercially important fin-fish such as California sheephead (*Semicossyphus pulcher*), and copper (*Sebastes caurinus*) and blue (*Sebastes mystinus*) rockfish. Each of these targeted species was the subject of prior bio-economic modeling related to the effects of MPAs in southern California (44, 52). Our analysis omits species from important invertebrate fisheries including red urchin (*Mesocentrotus franciscanus*) and spiny lobster (*Panulirus interruptus*) (but our methods could similarly be applied to these species given data). Non-targeted species include garibaldi (*Hypsypops rubicundus*), halfmoons (*Medialuna californiensis*), and blacksmith (*Chromis punctipinnis*) (See Table.S2 for a complete list of species). We used a Bayesian difference-in-difference regression to estimate any difference in mean total biomass densities of fin-fish species targeted by fishing effort (i.e., those potentially affected by an MPA) and those species not targeted by fishing before and after MPA implementation (51). The identification strategy control for unobserved environmental shocks to the system independent of the MPAs and similarly experienced by the targeted and non-targeted species. Conditional on the assumptions of the model, this regression produces an estimate of the effect of the MPAs on the mean total biomass densities of targeted species throughout the Channel Islands.

Consistent with MPA theory, over the first three years of implementation (2003-2006), the effects of the MPAs are unclear, with support for a small negative effect to a substantially positive effect, with much higher probability of a small positive effect (median estimated effect 32%, 90% credible interval 3% - 70%). Over the next six years the model estimates greater probabilities of an increasingly positive MPA effect, peaking in 2009-2011 with a median estimate of MPA effect of a 81% increase in mean total biomass density of targeted species (90% credible interval 41% - 133% (Fig.2). These empirical estimates are in line with the outcomes that our simulation model suggests are plausible. While this concordance between theory and empirics is



by no means proof of the robustness of our results, it is an important line of evidence. However, in the subsequent years the trend reverses itself, and for the years 2015-2017 we once again see no clear effect of the MPAs (median estimated effect -7%, 90% credible interval -30% - 24%.) Fig.2

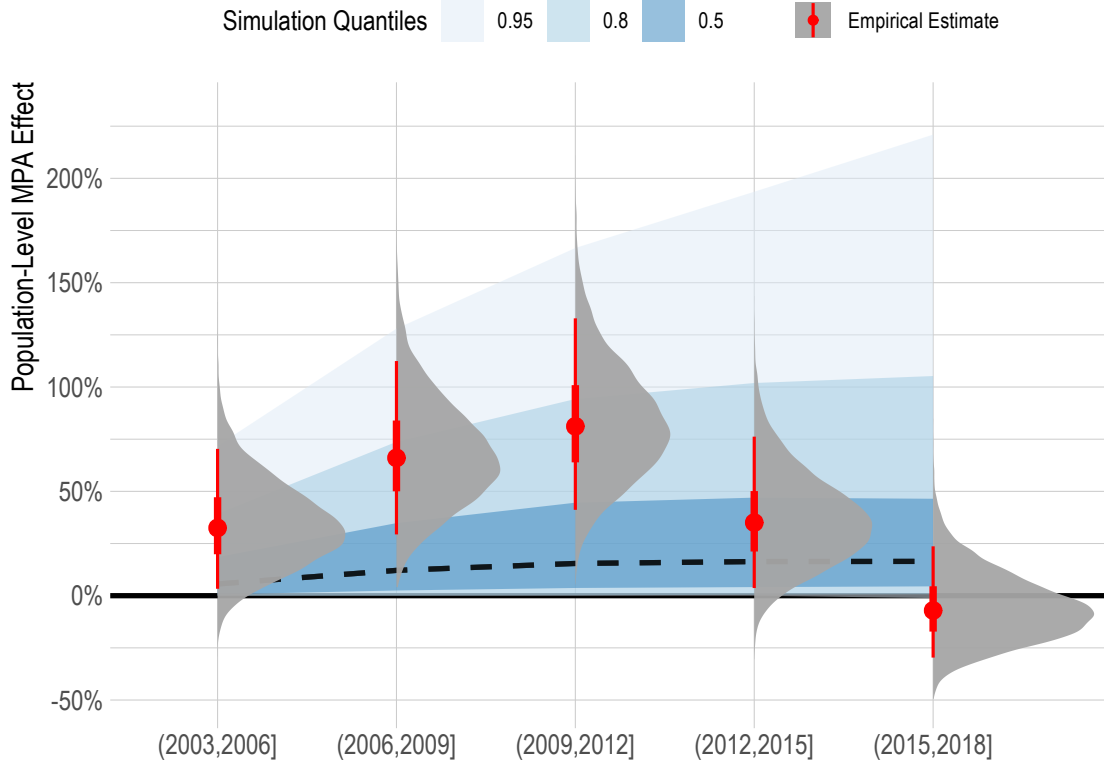


Figure 2: Results of difference-in-difference regression estimating the population effect of the Channel Island MPAs on mean total biomass densities of targeted species (difference in mean total biomass density of targeted species over time relative to expected levels using non-targeted species as a control). Grey distributions show posterior probability distribution of estimated MPA effect; red point is median estimated effect, thicker red section 50% credible interval, thinner red line 90% credible interval). Blue distributions in background show range of MPA effects produced by simulation model tuned to reflect the dynamics of the Channel Island MPAs (black dashed line is median simulated value). Results are estimated in blocks of three years, including years greater than or equal to left-hand value and less than right-hand value.

How can we explain the lack of a clear population-level MPA effect after over ten years of protection? One explanation may lie in fleet dynamics. Much of the theoretical literature on MPAs assumes that all else being equal larger reserves produce larger conservation gains (42). However, these models generally simulate fleet dynamics through fishing mortality rates (e.g. concentration of fishing mortality (53)). The implication of this is that total catches will scale with the size of the available population: if fishing effort moves outside the reserve, total catch will go down if the pool of fishable biomass available to the fleet is lower outside the

reserve.

Alternatively, though, fishers can pursue a “constant-catch” rather than an effort-based strategy. This is an important and, to our knowledge, unexplored fleet model in MPA simulation. Under the constant catch model, fishers have a catch objective, and exert as much (or little) effort as needed to achieve that objective. While a constant-catch greater than the maximum sustainable catch from the population is not possible over the long-term under the assumptions of our model, over the short-term a constant-catch scenario is possible. Subsistence fisheries may use a constant-catch style policy over the short-term, as they seek to ensure that their food needs are met. Industrial fisheries may have pre-arranged agreements with buyers to deliver set amounts of fish. Constant-catch dynamics might also occur in fisheries with constraining quotas that are not updated after the implementation of MPAs. While open-access fishing strategies can result in “scorched earth” scenarios where the only fish left are found inside the reserve, across 94% simulations the net effect of the reserves was still positive. Under a constant-catch scenario though, fishers have to fish much harder than before to get the same catch from a smaller part of the population, reducing the size structure of the population and subsequently causing net conservation loss under 70% of our constant-catch simulations. This is an important and often overlooked possibility, especially as MPAs are increasingly implemented in quota-managed fisheries (54).

While we do not have access to fine scale fishing data from the Channel Islands alone, reported catches for the species of interest in the Santa Barbara region exhibit a mix of stable, downward, and upward trajectories (see Fig.SXX) which indicates that a negative MPA effect caused by a constant-catch fishing strategy is unlikely. Instead, another possibility for the observed decline in Channel Islands MPA effects is environmental disturbance. The Channel Islands region (and the entire West coast of the USA) experienced a dramatic ‘marine heatwave’ beginning in 2014 and persisting through 2016, resulting in part in extremely elevated water temperatures throughout the region (55). Many of the non-targeted species in the Channel Islands have warm thermal affinities and have increased in numbers since the heatwave (56). The targeted group is made up mostly of fishes with cold-water affinities, such as members of the genus *Sebastes*. We hypothesize that the recent evidence for a decline in densities of targeted species is due to environmental conditions that disproportionately affect the targeted group (and not for example due to concentrated fishing pressure outside the reserves). The practical result of this is that in the presence of this marine heatwave the non-targeted species may no longer serve as an effective control for the evolution of biomass densities of targeted finfish in the absence of the MPAs (a violation of the “parallel trends” assumption required for Difference-in-difference models).

This hypothesis is supported by the fact that we estimate a similar decline in the estimated MPA effect both

inside and outside of the MPAs (Fig.SXX) (as well as observe the decline in the raw data, Fig.3). If the cause of recent declines was due to increases in fishing pressure we would expect to see substantial declines only in the fished areas. While we see evidence for the validity of the parallel trends assumption in the early years of our data (Fig.2, Fig.SXX), it is likely that the non-targeted species reacted in a different way to the marine heatwave than the targeted species did, causing a violation of the parallel trends assumption in the post 2014 data.

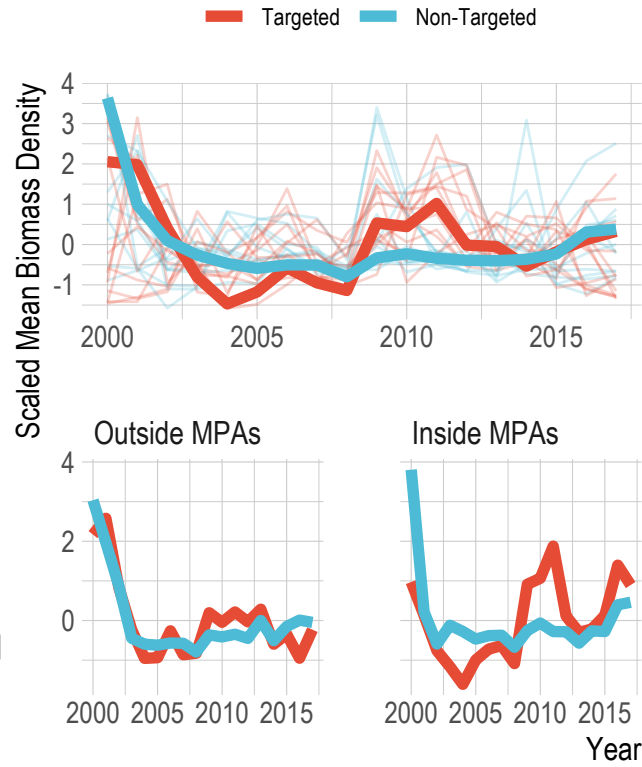


Figure 3: Centered and scaled trends in biomass densities of targeted and non-targeted finfish included in our study. Top panel shows trends across all sites, with smaller background lines showing trends for each individual species. Bottom two panels show aggregate biomass density trends outside and inside MPAs.

### 2.1.2 When Can We Detect the Effects of MPAs?

Containing a carefully designed, well-enforced, and well-studied MPA network, the Channel Islands would seem at face value to be an ideal location to study the population-level effects of protected areas. The persistently high response ratios suggest that despite overall decreases in targeted biomass densities inside and outside MPAs, the MPAs may still be providing protection within their borders. But, as we have shown here, these response ratios are not necessarily an indicator of broader population-level effects. The

difference-in-difference strategy utilized here presents an alternative identification strategy to response ratios , that while not without its own strict caveats presents some potential improvements over response-ratios as a means of estimating population-level effects. While we estimate an uncertain but overall positive effect of the MPA network in its first few years, we are unable to detect a robust signal from 2012-2017. We believe that the disappearance of increasing probabilities of positive MPA effects estimated by our model are likely driven by the marine heatwave experienced by the region beginning in 2014. This likely violation of the parallel trends assumption means that post 2014 estimates of MPA effects may be unreliable. After 14 years of MPA protection and following a large environmental perturbation we are left without a clear picture of the effect of the Channel Island MPA network on biomass densities of targeted fin-fish species from either response ratios or the difference-in-difference model.

Our simulation results suggest that we should not be surprised by this result. The Channel Islands MPAs cover 20% of the surface waters in the Channel Islands, and while formal stock assessments are not available for many of the targeted species in our analysis, what evidence we have suggests that, as a group, these fish are on average not heavily overfished. Some species, such as California sheephead and blue rockfish were likely below target levels during the period (48, 49), but projections based upon the overall average response across all species will likely suggest modest benefits even if a subset of species could experience much larger population gains. Our simulations suggest that the average percentage difference in densities of targeted species with and without MPAs to be modest (Fig.2). Effects of this size are likely to be challenging to detect empirically given the large natural variation of marine ecosystems (especially temperate reefs) and the observation error inherent in infrequent (e.g. annual) common in marine systems.

Our simulations and difference-in-difference model examine percentage changes in biomass densities (as oppose to changes in total population size). An increase in biomass densities from  $0.02\text{kg/m}^2$  to  $0.04\text{kg/m}^2$  would be produce as a 100% increase. While a large percentage effect, this is a small change in biomass densities relative to the variance in the observation process itself. While an MPA providing 25% protection might be expected to produce a 30% increase in biomass densities, expressed as a percentage of unfished biomass this gain is on the order of 15% (Fig.SXX). In addition, the median estimated age at sexual maturity for the targeted species included in this study is 6 years, meaning that the span of this analysis represents less than three generations of MPA protection for half of the the measured species. Ongoing monitoring may yet reveal clearer effects. Analysis of more rapidly growing and maturing species, e.g. spiny lobster, may also reveal clearer signals.

Given the natural variability of marine ecosystems, and the large challenges of obtaining accurate samples from oceanic environments, how large of an effect would an MPA network have to have in order to allow a

difference-in-difference strategy such as this to be a reliable measure of MPA effects? We simulated data from a range of scenarios with increasing MPA effect size, along with increasing degrees of observation error and natural recruitment variation. As an added measure, we include scenarios in which the sampled species go through recruitment regimes, which may be positive for both targeted and non-targeted species, or positive for non-targeted species and negative for targeted species. We then used a simple Bayesian difference-in-difference regression styled after the full model used here on these simulated data, and estimated the percent error between the posterior probability distribution of the estimated MPA effect and true simulated MPA effect.

While unbiased across simulations, the difference-in-difference model struggled severely when MPA effect sizes were less than 25% and the model was faced with observation and process errors (Fig.4). Even models fit to data generated from large effect sizes commonly misestimated the true MPA effect by 50% or more. Obtaining a mean absolute percent error (MAPE) of 25% or less across our simulated datasets required a population-level MPA effect of at least 30%. This is merely an illustrative exercise, omitting critical factors such as detection probability and sampling strategy. However, since nearly any omission which one can think of would make an MPA effect harder to detect, not easier, these results serve as a useful floor for the likely difficulty in estimating MPA effects. In the context of the Channel Islands, given the potential effect size produced by our simulation model these results suggest that we might expect to be unable to precisely estimate the true population-level effect of the MPAs.

When should we expect to see MPA effects big enough to stand a reasonable chance of detection? We simulated 9252 MPA scenarios across a wide range of life histories, network designs, and fishing dynamics (see SI for a full description of scenarios). Suppose that we are willing to tolerate a MAPE of 25%. Our analysis suggests that we would need an MPA effect size of at least 30% to achieve this. Two of the most critical drivers of MPA performance are the size of the MPA and the degree of fishing pressure. Looking across these two variables, if the MPA network covers 25% or more of a species range and pre-MPA depletion is greater than 60% we might expect an effect size with our target MAPE. While recently some extremely large MPAs have been enacted that may indeed reach into the higher levels of MPA coverage, for near-shore commercial fin-fish many MPA networks are likely to cover areas more in line with the Channel Islands (20%) or smaller, and as such have population-level effect sizes that may be difficult to detect (Fig.5-A).

The MPA literature highlights a large number of variables beyond simply size and fishing pressure that can affect performance. We examined the variability in expected MPA effects across each of the two major axes (pre-MPA depletion and MPA size). As both MPA size and pre-MPA depletion increase, the potential for a large MPA effect increases. However, for both variables even at extremely large or extremely small values a wide range of MPA effects were possible (though as we might expect the effect of pre-MPA depletion, in

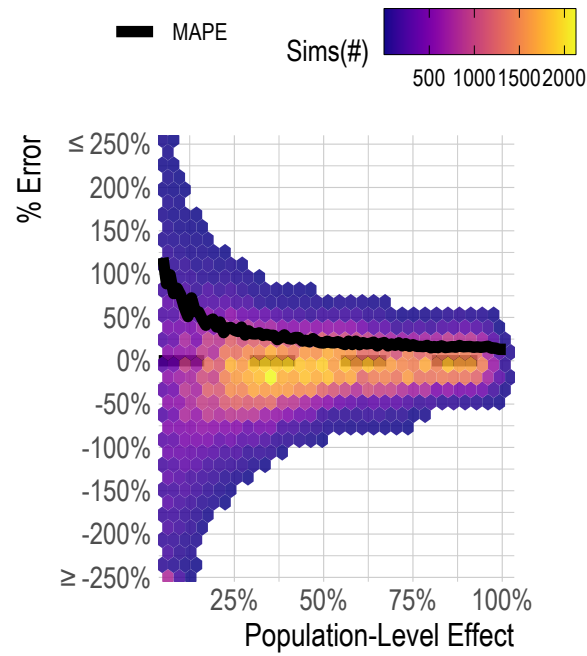


Figure 4: Distribution of percent error in posterior estimates of population-level MPA effect (y-axis) plotted against true simulated MPA effect (x-axis). Color shows concentration of simulations. Black line shows mean absolute percent error (MAPE) as a function of true simulated MPA effect.

other words fishing pressure, was much clearer than MPA size alone) (Fig.5-B).

To put these results into context, the FAO estimates that 7% of the worlds fisheries with status estimates fall into the relatively unexploited category (roughly depletion less than 50%), 60% fall into the fully fished category (roughly depletion 50%-70%), and 33% fall into the heavily fished category (roughly depletion greater than 70%) (57), though works that include a broader range of fisheries estimate that 50% or more of stocks to fall into the heavily fished category (59, 60). The population-level effects of MPA networks covering 25% or less of a species range may be difficult to detect in many places with already well-managed fisheries, while for that size we might expect clearer effects in less-managed locations (though that of course ignores the complication of compliance with MPA regulations). Within these broad guidelines a wide range of outcomes are possible based on local fleet and fish dynamics: as a starting place users can use the bio-economic MPA simulation model developed for this paper to explore potential outcomes for specific MPAs using an interactive web application available [here](#).

## Conclusions

MPAs are an important part of the marine resource management toolbox. Under ideal circumstances they can protect individual species and ecosystem linkages, while supporting local economies through tourism and fishing opportunities. One rationale for the expansion of MPAs is that they will deliver net conservation benefits both inside *and outside* their borders. To date, this assumption is insufficiently tested, and this is the focus of our paper. Our results show that population-level conservation benefits of MPAs are highly context dependent and in many circumstances, are likely to be small enough that they are nearly impossible to detect empirically. This is exactly what we found in our empirical case study from the relatively large and well-studied network of MPAs in the Channel Islands, California, USA.

A large theoretical literature has pointed out the importance of a wide range of economic and environmental factors in determining the effectiveness of MPAs (32, 40, 43). Our simulation model allows users to place this collective theory into context, clarifying under what states of the world we might expect to see particular effect sizes, and demonstrating what effect sizes we might reasonably expect to be detectable in the real world. In the case of the Channel Islands, simulation modeling suggests for the network in question, an effect size on the order of 30% or smaller is likely, which our analysis in turn demonstrates may be challenging to detect. This cautionary tale is likely to hold for many coastal MPA networks around the world.

Once simulation models have been used to help design an MPA, how can users evaluate whether it is achieving their objectives? Response ratios are commonly used as evidence for conservation outcomes of MPAs; (5) and

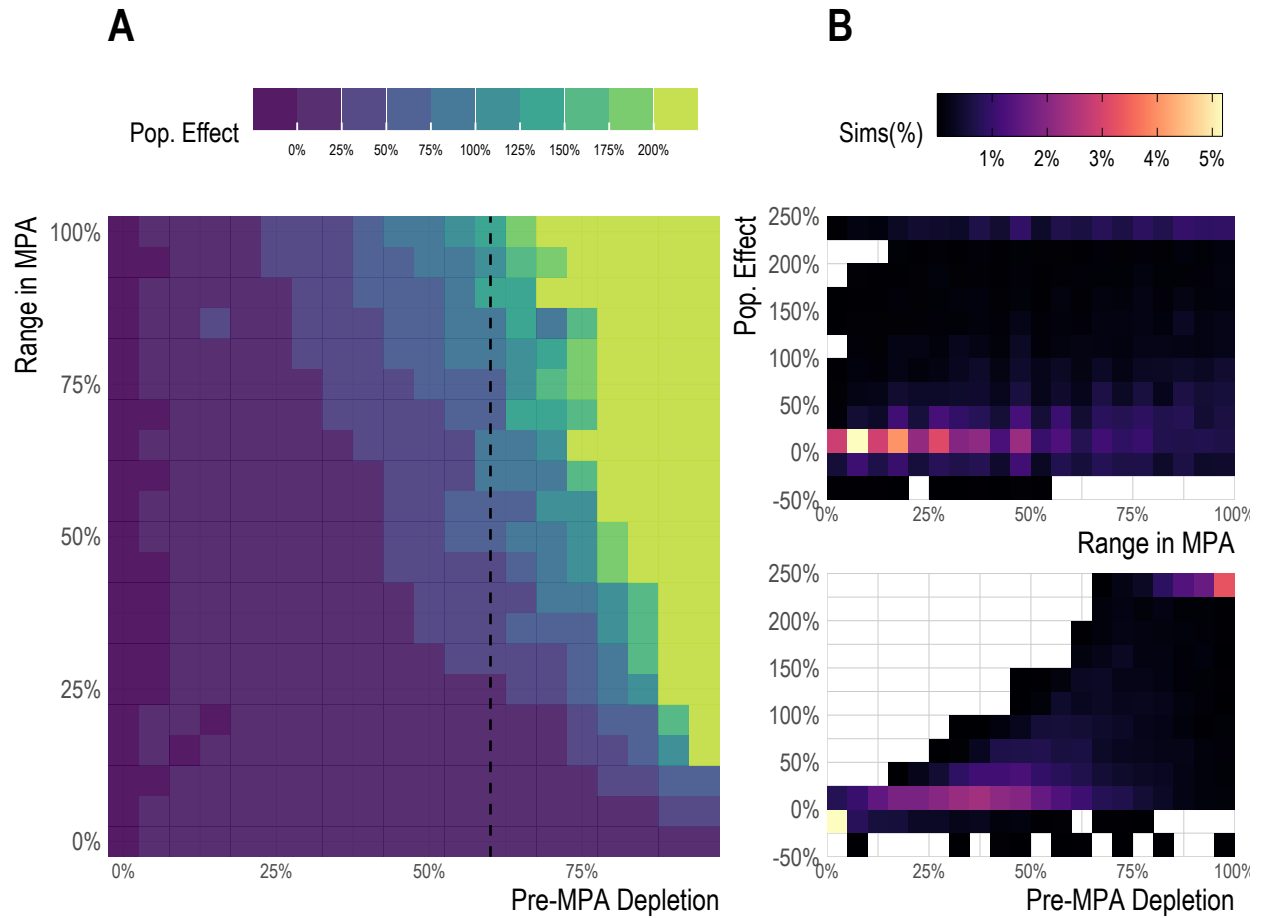


Figure 5: Simulated population-level (pop.) MPA effect sizes as a function of percent of species' range inside MPA (x-axis), and pre-MPA depletion (y-axis). Pre-MPA depletion is a measure of fishing pressure, where 0 means that the population is unfished, and 1 means that the population is extinct in the time period immediately prior to MPA implementation. Panel A) shows median MPA effects across range in MPA and pre-MPA depletion Panel B) shows distribution of simulations across range of MPA size and pre-MPA depletion separately.



(61) present meta-analyses of hundreds of such studies. These results often find massively higher densities and biomass inside MPAs than outside (5). But as suggested in (42), (50), (51) and further demonstrated here, without careful attention to the design of control sites (e.g. accounting for the displacement of fishing effort by MPAs), response ratios may be highly unreliable estimators of population-level MPA effects. When MPAs affect nearby control sites used in response ratios through biological spillover or concentration of fishing effort, it is entirely possible for MPA to produce massive response ratios while simultaneously having minimal effects on the entire population partially protected by the MPAs (and *vice versa*. As (51) suggests, there are many potential alternatives for estimating the effects of MPAs that better account for the challenges of causal inference (though that may be more data-intensive). We applied one such approach here (a difference-in-difference estimator), and yet were still unable to reach robust conclusions as to the effect of MPAs on the biomass density of targeted finfish in the Channel Islands, due to the likely small size of the true effect relative to the influence of environmental variability. If pre-MPA data are available, data currently used in response ratios can easily be re-purposed for an analysis such as this one; we encourage holders of such data worldwide to conduct similar exercises to examine to what extent other empirical estimates of population-level MPA effects conform to MPA theory.

While this does not mean that all MPAs will face similar challenges in estimating their effects, our results in the relatively large, well-enforced, and rigorously studied (though also relatively lightly fished) Channel Islands Marine Protected Area network make clear that in many instances empirically detecting a clear effect of MPAs on total biomass densities of targeted finfish at the population level may not be possible. How then should stakeholders go about adaptively monitoring and managing MPAs? Simulation modeling incorporating the diverse drivers represented here can help inform the range of effect sizes that may be expected, and monitoring programs can perhaps be tuned to focus on the species groups that have the highest chance of a detectable effect size over the early years of the reserve (62). Expanding data collection to include robust monitoring of spatio-temporal fleet dynamics may help assess the validity of control sites used in response ratios, support the direct inclusion of these fleet dynamics into statistical models, and allow managers to take into account potential negative interactions between MPAs and fleet dynamics such as those that may occur under constant-catch dynamics. Whenever possible monitoring programs should be implemented prior to MPA implementation to provide a pre-treatment benchmark.

Stock assessment models (63) that account for the population within the MPAs (64) may be able to answer the management relevant question of whether fishing mortality rates and biomass levels from systems containing MPAs are in-line with management objectives (62). However, such an approach does not necessarily shed light on whether the MPAs themselves caused the estimated state of the population, and of course are highly data

intensive, potentially restricting our ability to provide stock-assessment based inference of MPA outcomes for broad arrays of targeted species.

Non-equilibrium analyses also help set expectations for effect sizes over time (62). Educating communities about the challenges of estimating the effects of MPAs can help set expectations, so that a lack of a clear effect is not necessarily viewed as a failure of the program, or large positive result based solely on response ratios as a clear sign of success and subsequent relaxation of other fishery management strategies. Rather, results and subsequent management actions (such as adaptation of MPA networks) must be considered in the context of reasonable expectations given the size, age, and degree of enforcement of the MPAs in question, together with the ecological and economic dynamics of a given system. While this paper has focused on the conservation outcomes of MPAs, future work must also address the challenge of predicting and estimating the fishery impacts of protected areas.

As the number and size of global MPA networks increase, it is critical that we both set appropriate expectations for their outcomes, and plan how we will monitor the performance of these protected areas over time. While the history of MPA science has made important strides in helping us understand the dynamics of protected areas, the future of MPA science must directly tackle the challenge of evaluating the performance of these MPAs at the regional scale, a task which has to date not been widely addressed. This is particularly true if communities are depending on MPAs as their primary marine resource management tool. Commonly employed metrics such as response ratios may be applicable in some circumstances, for example, when an MPA is designed for food security in the face of a disaster or for protection of unique or threatened species inside its borders, but can have shortcomings as metrics of population-level effects. Dependence on unreliable estimators of MPA effects may lead to stakeholders incorrectly attributing negative environmental shocks as MPA failures, or interpreting data arising from scorched-earth fishing outside MPAs as a conservation success. Both of these scenarios would hinder the ability of MPAs to serve as effective marine resource management tools at scale. Bio-economic modeling can help frame community expectations, reducing the potential for a reduction in support if unrealistic conservation or fishery expectations are not realized. Statistical approaches that explicitly address complications such as the spatial spillover effects of MPAs (such as the difference-in-difference approach used here) may give users an improved understanding of the performance of their MPAs, but even they may struggle when expected effect sizes are small. Clearly communicating what we should expect, and what we can detect, from MPAs is critical in ensuring that MPAs play effective roles in fisheries management and marine conservation.

## 2.2 Materials and Methods

We present here critical characteristics of our simulation model and regression approach. Further details can be found in the Supplementary Information. All analysis were conducted in R (66). Our main difference-in-difference model was fit using Stan (67) using the `rstanarm` package (68). All materials needed to replicate results can be found [here](#).

### 2.2.1 Simulation Model

Our bio-economic model simulates the effect of MPAs on a spatially explicit age-structured representation of a single species. Readers can explore the functionality of the model using an online tool available [here](#). Full details of the simulation model are available in the Supplementary Information.

### 2.2.2 Difference in Difference Regression

The difference-in-difference model used empirical kelp forest survey data from the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO) monitoring in the Northern Channel Islands. A network of MPAs covering approximately 20% of the islands' waters was put in place in 2003 as part of the California Marine Life Protection Act (MLPA) (see (22), (23), (24), and (25) for information on the creation of the MLPA). PISCO conducts visual SCUBA surveys at a large number of rocky-reef and kelp forest sites inside and outside of MPAs throughout the Channel Islands, producing estimates of densities of fishes that are both targeted and non-targeted by fishing (Fig.6). The details of the monitoring program are described in (26).

The key assumptions of the difference-in-difference model are that a) within the time-frame of the model there are no significant interaction effects between the targeted and non-targeted species (which in fact we do not detect, see SI), and b) that in the absence of the MPAs both the targeted and non-targeted groups of species would have exhibited similar trends in densities. It is important to note that the model is agnostic as to the root causes of the parallel trends, so long as they hold.

The regression amounts to estimating the pre-post MPA difference in the biomass densities of targeted species minus the same difference for non-targeted species in the Channel Islands.

The simplified form of this model is

$$d_i \sim \text{Gamma}(e^{\beta_0 + \beta_1 T_i + \beta_2 MPA_i + \beta_3 T_i MPA_i + \mathbf{B}^c \mathbf{X}_i + \mathbf{B}^s \mathbf{S}_i}, \text{shape}, \text{scale}) \quad (1)$$

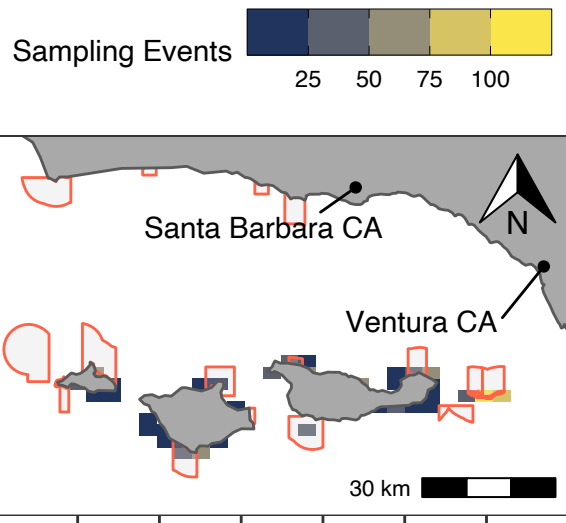


Figure 6: Map of study region; the Northern Channel Islands, California, USA. Colors show binned number of PISCO sampling events across the time period of our study.

where  $d_i$  is the biomass density at observation  $i$ ,  $T$  indicates whether the observation  $i$  is for a targeted ( $T = 1$ ) or non-targeted ( $T = 0$ ) species, and  $MPA$  marks whether observation  $i$  is in a pre MPA ( $MPA = 0$ ) or post MPA ( $MPA = 1$ ) state.  $\mathbf{B}^c$  is a vector of coefficients for additional control variables in matrix  $X$  such as water visibility and observer experience.  $\mathbf{B}^s$  is a vector of hierarchical coefficients for each sampling location  $\mathbf{S}$ , clustered by island. Under the assumptions of this model,  $\beta_3$  is the causal effect of the treatment ( $MPA$ ) on the treated (targeted species).  $\beta_0$  is the mean total biomass of non-targeted species pre-MPA, and  $\beta_1 T$  is the mean total biomass of targeted species pre-MPA.  $\beta_2 MPA$  is the effect of the post-MPA period on the non-targeted species. The shape and scale parameters of the Gamma distribution are estimated as well. See SI for further details of the estimation model. 46% of the samples in the raw data come from within MPAs, while the MPAs themselves cover 20% of the surface waters of the Channel Islands. As such, we weight each observation such that within MPA data are assigned a total weight of 0.2 and outside-MPA data a total weight of 0.8. See SI for sensitivity analyses of various model structures and synthetic controls results. We briefly assess two of the most critical assumptions of this model here: that the treated and non-treated groups have parallel trends, and that the effect of the treatment on the treated does not tangentially affect the untreated. While the parallel trends assumption cannot be formally proven, we can examine its validity using the data from the years before the MPAs were put in place in 2003. We do not detect any significant differences in the trends of the biomass densities of the targeted and non-targeted species in the years before the MPAs (Fig.SXX). However, we believe that the parallel trends assumption is likely violated in the post 2014 data.

With regards to the second assumption, all of the species in this empirical analysis exist within an ecosystem, and as such affect each other through mechanisms such as predation, competition, and habitat modification. We find it unlikely that these effects have had enough time to manifest in a meaningful way in the 14 years of post-MPA data used in our analysis (69, 70). We used convergent cross mapping (CCM), in the manner of (71), to test for the possibility of the trophic cascades biasing our results. Our results found no significant cross-mappings between targeted and non-targeted species, indicating that while clearly there are interactions between these groups on some level, the effects within the timespan of the data are not pronounced enough to be of concern to our results (Fig.SXX). However, the longer MPAs are in place, the greater the possibility that substantial species interactions that can affect use of non-targeted species as a control may arise.

1. Johannes RE (1978) Traditional Marine Conservation Methods in Oceania and Their Demise. *Annual Review of Ecology and Systematics* 9(1):349–364.
2. IUCN (1976) *IUCN yearbook, 1975-76 : Annual report of the International Union for Conservation of Nature and Natural Resources for 1975 and for January-May 1976.*

3. Watson JEM, Dudley N, Segan DB, Hockings M (2014) The performance and potential of protected areas. *Nature* 515(7525):67–73.
4. Gaines SD, White C, Carr MH, Palumbi SR (2010) Designing Marine Reserve Networks for Both Conservation and Fisheries Management. *Proceedings of the National Academy of Sciences* 107(43):18286–18293.
5. Lester SE, et al. (2009) Biological effects within no-take marine reserves: A global synthesis. *Marine Ecology Progress Series* 384:33–46.
6. Halpern BS, Warner RR (2003) Review Paper. Matching marine reserve design to reserve objectives. *Proceedings of the Royal Society of London Series B: Biological Sciences* 270(1527):1871–1878.
7. Edgar GJ, et al. (2014) Global conservation outcomes depend on marine protected areas with five key features. *Nature* 506(7487):216.
8. Gerber LR, Heppell SS, Ballantyne F, Sala E (2005) The role of dispersal and demography in determining the efficacy of marine reserves. *Canadian Journal of Fisheries and Aquatic Sciences* 62(4):863–871.
9. Goni R, Hilborn R, D'iaz D, Mallol S, Adlerstein S (2010) Net contribution of spillover from a marine reserve to fishery catches. *Mar Ecol Prog Ser* 400:233–243.
10. Halpern BS, Lester SE, Kellner JB (2009) Spillover from marine reserves and the replenishment of fished stocks. *Environmental Conservation* 36(04):268–276.
11. Kay MC, Lenihan HS, Kotchen MJ, Miller CJ (2012) Effects of marine reserves on California spiny lobster are robust and modified by fine-scale habitat features and distance from reserve borders. *Marine Ecology Progress Series* 451:137–150.
12. Stobart B, et al. (2009) Long-term and spillover effects of a marine protected area on an exploited fish community. *Marine Ecology Progress Series* 384:47–60.
13. McClanahan TR, Mangi S (2000) Spillover Of Exploitable Fishes From A Marine Park And Its Effect On The Adjacent Fishery. *Ecological Applications* 10(6):1792–1805.
14. Russ G, Alcala A (1996) Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. *Marine Ecology Progress Series* 132:1–9.
15. Thompson AR, Chen DC, Guo LW, Hyde JR, Watson W (2017) Larval abundances of rockfishes that were historically targeted by fishing increased over 16 years in association with a large marine protected area. *Royal Society Open Science* 4(9):170639.

- 506 16. Baetscher DS, et al. (2019) Dispersal of a nearshore marine fish connects marine reserves and adjacent  
507 fished areas along an open coast. *Molecular Ecology* 28(7):1611–1623.
- 508 17. Pelc R, Baskett M, Tanci T, Gaines S, Warner R (2009) Quantifying larval export from South African  
509 marine reserves. *Marine Ecology Progress Series* 394:65–78.
- 510 18. Costa BH e, et al. (2013) Fishers' Behaviour in Response to the Implementation of a Marine Protected  
511 Area. *PLOS ONE* 8(6):e65057.
- 512 19. Mason J, Kosaka R, Mamula A, Speir C (2012) Effort changes around a marine reserve: The case of the  
513 California Rockfish Conservation Area. *Marine Policy* 36(5):1054–1063.
- 514 20. Murawski SA, Wigley SE, Fogarty MJ, Rago PJ, Mountain DG (2005) Effort distribution and catch  
515 patterns adjacent to temperate MPAs. *ICES Journal of Marine Science* 62(6):1150–1167.
- 516 21. McDermott GR, Meng KC, McDonald GG, Costello CJ (2019) The blue paradox: Preemptive overfishing  
517 in marine reserves. *Proceedings of the National Academy of Sciences* 116(12):5319–5325.
- 518 22. Osmond M, Airame S, Caldwell M, Day J (2010) “Lessons for marine conservation planning: A comparison  
519 of three marine protected area planning processes”. *Ocean & Coastal Management* 53(2):41–51.
- 520 23. Kirlin J, et al. (2013) California's Marine Life Protection Act Initiative: Supporting implementation  
521 of legislation establishing a statewide network of marine protected areas. *Ocean & Coastal Management*  
522 74:3–13.
- 523 24. Botsford LW, White JW, Carr MH, Caselle JE (2014) Chapter Six - Marine Protected Area Networks  
524 in California, USA. *Advances in Marine Biology*, Marine Managed Areas and Fisheries., eds Johnson ML,  
525 Sandell J (Academic Press), pp 205–251.
- 526 25. Hilborn R (2012) The role of science in MPA establishment in California: A personal perspective.  
527 *Environmental Conservation* 39(03):195–198.
- 528 26. Caselle JE, Rassweiler A, Hamilton SL, Warner RR (2015) Recovery trajectories of kelp forest animals are  
529 rapid yet spatially variable across a network of temperate marine protected areas. *Scientific reports* 5:14102.
- 530 27. Gaines SD, Gaylord B, Largier JL (2003) Avoiding Current Oversights in Marine Reserve Design.  
531 *Ecological Applications* 13(sp1):32–46.
- 532 28. Botsford LW, et al. (2008) Connectivity, sustainability, and yield: Bridging the gap between conventional  
533 fisheries management and marine protected areas. *Reviews in Fish Biology and Fisheries* 19(1):69–95.

- 534 29. Di Franco A, et al. (2018) Linking home ranges to protected area size: The case study of the Mediterranean  
535 Sea. *Biological Conservation* 221:175–181.
- 536 30. McGilliard CR, Hilborn R (2008) Modeling no-take marine reserves in regulated fisheries: Assessing the  
537 role of larval dispersal. *Canadian Journal of Fisheries and Aquatic Sciences* 65(11):2509–2523.
- 538 31. Burgess SC, et al. (2014) Beyond connectivity: How empirical methods can quantify population  
539 persistence to improve marine protected-area design. *Ecological Applications* 24(2):257–270.
- 540 32. Hilborn R, Punt AE, Orensanz J (2004) Beyond band-aids in fisheries management: Fixing world fisheries.  
541 *Bulletin of Marine Science* 74(3):493–507.
- 542 33. Hilborn R (1992) Can fisheries agencies learn from experience? *Fisheries* 17(4):6–14.
- 543 34. Walters CJ, Martell SJ (2004) *Fisheries ecology and management* (Princeton University Press).
- 544 35. Hastings A, Botsford LW (2003) Comparing Designs Of Marine Reserves For Fisheries And For Biodiversity.  
545 *Ecological Applications* 13(sp1):65–70.
- 546 36. Gerber LR, et al. (2003) Population Models For Marine Reserve Design: A Retrospective And Prospective  
547 Synthesis. *Ecological Applications* 13(sp1):47–64.
- 548 37. Hilborn R, et al. (2004) When can marine reserves improve fisheries management? *Ocean & Coastal*  
549 *Management* 47(34):197–205.
- 550 38. Botsford LW, Micheli F, Hastings A (2003) Principles for the Design of Marine Reserves. *Ecological*  
551 *Applications* 13(sp1):25–31.
- 552 39. Smith MD, Wilen JE (2003) Economic impacts of marine reserves: The importance of spatial behavior.  
553 *Journal of Environmental Economics and Management* 46(2):183–206.
- 554 40. Smith K (2006) Distributions, relative abundances and reproductive biology of the deep-water crabs  
555 *Hypothalassia acerba* and *Chaceon bicolor* in southwestern Australia.
- 556 41. Walters C, Pauly D, Christensen V, Kitchell JF (2000) Representing Density Dependent Consequences of  
557 Life History Strategies in Aquatic Ecosystems: EcoSim II. *Ecosystems* 3(1):70–83.
- 558 42. White JW, et al. (2011) Linking models with monitoring data for assessing performance of no-take  
559 marine reserves. *Frontiers in Ecology and the Environment* 9(7):390–399.
- 560 43. White JW, Botsford LW, Moffitt EA, Fischer DT (2010) Decision analysis for designing marine protected  
561 areas for multiple species with uncertain fishery status. *Ecological Applications* 20(6):1523–1541.



- 562 44. Costello C, et al. (2010) The Value of Spatial Information in MPA Network Design. *Proceedings of the*  
563 *National Academy of Sciences* 107(43):18294–18299.
- 564 45. Thorson JT, Munch SB, Cope JM, Gao J (2017) Predicting life history parameters for all fishes worldwide.  
565 *Ecological Applications*:n/a–n/a.
- 566 46. Love MS (2011) *Certainly more than you want to know about the fishes of the Pacific Coast: A postmodern*  
567 *experience* (Really Big Press, Santa Barbara, Calif.).
- 568 47. Rassweiler A, Costello C, Siegel DA (2012) Marine protected areas and the value of spatially optimized  
569 fishery management. *Proceedings of the National Academy of Sciences* 109(29):11884–11889.
- 570 48. Alonzo S, Key M, Ish T, MacCall AD (2004) *Status of the California Sheephead Stock for 2004*.
- 571 49. Dick EJ, et al. (2017) *The Combined Status of Blue and Deacon Rockfishes in U.S. Waters off California*  
572 *and Oregon in 2017* (Pacific Fishery Management Council, Portland, OR).
- 573 50. Ferraro PJ, Sanchirico JN, Smith MD (2018) Causal inference in coupled human and natural systems.  
574 *Proceedings of the National Academy of Sciences*:201805563.
- 575 51. Larsen AE, Meng K, Kendall BE (2019) Causal analysis in controlImpact ecological studies with  
576 observational data. *Methods in Ecology and Evolution* 0(0). doi:[10.1111/2041-210X.13190](https://doi.org/10.1111/2041-210X.13190).
- 577 52. Rassweiler A, Costello C, Hilborn R, Siegel DA (2014) Integrating scientific guidance into marine spatial  
578 planning. *Proceedings of the Royal Society B: Biological Sciences* 281(1781):20132252.
- 579 53. Halpern BS, Gaines SD, Warner RR (2004) Confounding effects of the export of production and the  
580 displacement of fishing effort from marine reserves. *Ecological Applications* 14(4):1248–1256.
- 581 54. Liu OR, Kleisner KM, Smith SL, Kritzer JP (2018) The use of spatial management tools in rights-based  
582 groundfish fisheries. *Fish and Fisheries* 19(5):821–838.
- 583 55. Gentemann CL, Fewings MR, García-Reyes M (2017) Satellite sea surface temperatures along the West  
584 Coast of the United States during the 20142016 northeast Pacific marine heat wave. *Geophysical Research*  
585 *Letters* 44(1):312–319.
- 586 56. Freedman R (2019) Understanding the Efficacy of Spatial Management on Emerging Threats. PhD thesis  
587 (University of California, Santa Barbara).
- 588 57. FAO ed. (2018) *The state of world fisheries and aquaculture* (Rome).
- 589 58. Thorson JT, Cope JM, Branch TA, Jensen OP (2012) Spawning biomass reference points for exploited  
590 marine fishes, incorporating taxonomic and body size information. *Canadian Journal of Fisheries and Aquatic*

591 *Sciences* 69(9):1556–1568.

592 59. Costello C, Gaines S, Gerber LR (2012) Conservation science: A market approach to saving the whales.  
593 *Nature* 481(7380):139–140.

594 60. Rosenberg AA, et al. (2018) Applying a New Ensemble Approach to Estimating Stock Status of Marine  
595 Fisheries around the World. *Conservation Letters* 11(1):e12363.

596 61. Halpern BS, Warner RR (2002) Marine reserves have rapid and lasting effects. *Ecology Letters* 5(3):361–  
597 366.

598 62. Nickols KJ, et al. (2019) Setting ecological expectations for adaptive management of marine protected  
599 areas. *Journal of Applied Ecology* 0(0). doi:[10.1111/1365-2664.13463](https://doi.org/10.1111/1365-2664.13463).

600 63. Hilborn R, Walters CJ (1992) *Quantitative Fisheries Stock Assessment* (Springer US, Boston, MA)  
601 doi:[10.1007/978-1-4615-3598-0](https://doi.org/10.1007/978-1-4615-3598-0).

602 64. Field JC, Punt AE, Methot RD, Thomson CJ (2006) Does MPA mean “Major Problem for Assessments”?  
603 Considering the consequences of place-based management systems. *Fish and Fisheries* 7(4):284–302.

604 65. Kaplan KA, et al. (2019) Setting expected timelines of fished population recovery for the adaptive  
605 management of a marine protected area network. *Ecological Applications* 29(6):e01949.

606 66. R Core Team (2019) R: A Language and Environment for Statistical Computing.

607 67. Carpenter B, et al. (2017) Stan : A Probabilistic Programming Language. *Journal of Statistical Software*  
608 76(1). doi:[10.18637/jss.v076.i01](https://doi.org/10.18637/jss.v076.i01).

609 68. Goodrich B, Ali I, Brilleman S (2020) Rstanarm: Bayesian applied regression modeling via Stan.

610 69. Babcock RC, et al. (2010) Decadal trends in marine reserves reveal differential rates of change in direct  
611 and indirect effects. *Proceedings of the National Academy of Sciences* 107(43):18256–18261.

612 70. Pershing AJ, et al. (2015) Slow adaptation in the face of rapid warming leads to collapse of the Gulf of  
613 Maine cod fishery. *Science* 350(6262):809–812.

614 71. Clark AT, et al. (2015) Spatial convergent cross mapping to detect causal relationships from short time  
615 series. *Ecology* 96(5):1174–1181.