Assessing the Population-Level Conservation Effects of Marine Protected Areas

Marine Protected Areas (MPAs) cover 3-7% of the world's ocean, and international organizations call for 30% by 2030. 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. We examine the conditions under which MPAs can provide population-level conservation benefits inside and outside their borders, and show that even in cases where the population 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 using a Bayesian difference-in-difference approach. We show that MPA effect sizes less than 30% are likely to be difficult to detect (even when they are present); smaller effect sizes (which we find are common) are even harder to detect. Our results provide a novel assessment of the population-level effects of a large and iconic Marine Protected Area network, and provide guidance for communities charged with monitoring and adapting MPAs.

Introduction

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 (Johannes 1978). Modern MPAs were first established as marine analogs to the terrestrial protection of iconic landscapes (IUCN 1976). Recent international efforts to expand MPAs, such as The International Union for

Conservation of Nature's 30% by 2030 MPA targets are based in part on the assumption that well-designed MPAs will not only provide conservation benefits inside their borders, but also have broader conservation effects on unprotected areas surrounding the MPAs, whether MPAs are designed explicitly for conservation, fishery benefits, or both (Gaines et al. 2010).

The empirical MPA literature has focused on assessing the ability of MPAs to provide conservation gains within their borders (Lester et al. 2009; Edgar et al. 2014). However, as conservation benefits accrue inside MPAs, MPAs also 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. Therefore, MPAs contribute to both local and regional population-level effects. Numerous factors influence how MPAs affect fish populations. These include the scale of adult and larval dispersal relative to the size of the MPAs (Gaines et al. 2003), the strength, timing, and location of density dependence (Burgess et al. 2014), the design of the network (Gaines et al. 2010; Rassweiler et al. 2014),the degree of enforcement (Edgar et al. 2014), the level of fishing pressure, the time span under evaluation, and how fishing and management responds to the implementation of the MPAs (Walters et al. 2000; Botsford et al. 2003; Gerber et al. 2003; Smith & Wilen 2003; Hilborn et al. 2004; Gaines et al. 2010; White et al. 2011; Moffitt et al. 2013; Ovando et al. 2016; Jaco & Steele 2020).

This largely theoretical literature is generally based on modeling of closed populations with some fraction protected inside of MPAs. In contrast to this population paradigm used in MPA simulations, MPAs are often evaluated empirically at local scales using spatial response ratios, commonly measured as the ratio of biomass densities (weight of organisms per unit area) of species inside relative to selected control sites outside of MPAs (Halpern 2003; Lester et al. 2009; Edgar et al. 2014; Caselle et al. 2015). These studies found clear evidence that well enforced and sufficiently sized MPAs are associated with high response ratios. Several studies have also documented empirical evidence for the existence of adult or larval fish spillover affecting fish abundance (Russ & Alcala 1996; McClanahan & Mangi 2000; Halpern et al. 2009; Kay et al. 2012). Where response ratios are available before and after MPA implementation, spatial before-after-control-impact (BACI) style studies have shown similarly clear and positive results (Thiault et al. 2019).

While these studies have clearly demonstrated the ability of MPAs to create differences between local fished and unfished areas, this body of empirical work does not necessarily serve as sufficient evidence for the population-level effects of MPAs. These spatial studies rely on assuming that selected control sites serve as a measure of what would have happened in the absence of MPAs. Control sites used in calculating response ratios are often selected based on habitat characteristics to justify their use as counterfactuals (Ferraro et al. 2018). However, beyond habitat differences, the very spillover effects MPAs are increasingly hoped to produce can negate the ability of spatial response ratio or BACI designs to accurately estimate the effects of MPAs. Export of adults or larvae from MPAs to “control” sites can affect their status as controls, as does displacement of fishing effort from MPAs to control sites. These factors can bias estimators of population-level effects like response ratios that require that the control sites are unaffected by the treatment (Moffitt et al. 2013; Ferraro et al. 2018). Control sites sufficiently far from MPAs to negate both spillover of fish or larvae and concentration of the fishing fleet could be selected, but finding suitably distant sites that are also appropriate proxies for the ecological and economic context of the MPAs is challenging. As variations of spatial response ratios and BACI studies have been a primary source of evidence for the conservation effects of MPAs, this means that our empirical understanding of the population-level impacts of MPAs is surprisingly limited.

In this paper, we present a paired theoretical and empirical assessment demonstrating the challenges in assessing the population-level impacts of MPAs. In 2003, a network of MPAs was established in the Channel Islands National Marine Sanctuary, California, USA (hereafter the Channel Islands) covering approximately 20% of the Islands' waters. The network has been used as a model case study in protected area design around the world (Botsford et al. 2014). We use data from the first 14 years of protection in a difference-in-difference (DiD) model (Angrist & Pischke 2009) to provide what is to our knowledge the first empirical assessment of the population-level effect of a large MPA network on a wide array of fin-fish species. Rather than relying on spatial controls as is typically done in MPA studies, we use groups of species targeted and not-targeted by fishing pressure as our treatment and control groups. In contrast to clear differences in biomass densities observed inside and outside of well-protected MPAs both globally (Lester et al. 2009) and in the Channel Islands (Caselle et al. 2015) we are unable to detect a clear population effect from the Channel Islands MPAs. We build off of existing MPA theory to consider why this might be, and provide guidance for scientists and managers as to when and how we might expect to estimate the population-level conservation effects of MPAs.

METHODS

Our methods consist of a spatially-explicit bio-economic simulation model and a Bayesian DiD regression (Angrist & Pischke 2009; McElreath 2020). DiD is a regression-based approach akin to BACI, assessing changes in control and treatment groups before and after treatment (Larsen et al. 2019). We used a bio-economic simulation model to provide theoretical expectations of population-level effects of MPAs, which we then confront with the empirical results from our DiD regression.

All analysis were conducted in R (R Core Team 2019). Our DiD regression was fit using Stan (Carpenter et al. 2017) through the `rstanarm` package (Goodrich et al. 2020). All data and code needed to fully reproduce this manuscript are publicly available at github.com/DanOvando/population-effects-of-mpas. A detailed description of the simulation model structure, as well as sensitivity analyses of our estimation model, are available in the online Appendix Supporting Information 1.

SIMULATION MODEL

Our bio-economic model simulates the effect of MPAs on a spatially explicit age-structured representation of a fish population. Readers can explore the functionality of the model using an online tool available at danovando.shinyapps.io/simmpa/. The purpose of the simulation model is to both set expectations for our empirical results, and to demonstrate the ways in which ecological and economic dynamics can interact to produce a wide range of population-level MPA effects. The full range of factors explored are shown in Table.1, and the equations of the simulation model can be viewed in the Appendix S1 Section 2. We used this model to generate 10168 simulated MPA outcomes across 7618 species.

Many papers have presented simulation analyses of MPA outcomes (Fulton et al. 2015). Our model incorporates core ecological and economic drivers of MPA performance assessed by these individual papers into a cohesive model, similar in spirit to Krueck et al. (2017). The simulation model consists of 50 patches with wrapped edges. For each simulation we first randomly pull a species and its associated life history traits from the FishLife (Thorson et al. 2017) package. We pair these data with randomly selected values governing the characteristics of the simulation (Table.1). Key choices available to the model include parameters governing fishing pressure and MPA design. For a given simulation, the model randomly selects a fleet model and fishing effort allocation strategy. The fleet model can either be constant-catch (the fleet exerts as much effort as needed to maintain a fixed amount of catch), constant-effort (the fleet maintains a constant amount of effort over time), or open-access (fishing effort of the fleet expands and contracts in response to available profits). The total fishing effort exerted by the fleet can then be distributed in space uniformly, in proportion to spatial catch per unit effort, or in proportion to spatial profit per unit effort.

The simulation then begins to apply the fleet model to the population, and in a randomly selected year implements an MPA network. The model samples a percentage of the population's range to place in MPAs, and randomly assigns patches to MPAs either across a uniform system or preferentially on higher-quality habitat. The model then randomly selects whether fishing effort that used to operate inside the MPAs is redistributed to the areas outside the MPAs, or leaves the fishery entirely. We then continue the simulations with the MPAs in place. Each simulation is paired with a simulation identical in every way except that MPAs are not implemented (i.e., a simulated control). We then calculate the effect of the MPAs on the population as the difference in biomass densities in the simulation with MPAs relative to biomass densities in the simulation without MPAs.

These simulation results provide a library of plausible MPA effects for a range of biological and economic assumptions. One set of simulations was specifically designed to reflect the dynamics of the subset of species available in the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO) monitoring data from the Channel Islands used in this study. For this set we only include species of the same genus as those targeted by fishing in the PISCO data, restrict fishing pressure such that the simulated populations are moderately to lightly exploited (since the PISCO data used here excludes deeper-water species such as boccacio, *Sebastes paucispinis*, which were overexploited at the inception of the Channel Island MPAs, and threatened invertebrates such as red abalone *Haliotis rufescens*), and cap the MPA size at 20% of the population's range (Rassweiler et al. 2012). For each of these Channel Island style simulations, we calculated 1) the 'true' population-wide difference in biomass between the simulations with and without the MPAs and 2) the response ratio of biomass densities inside and outside the simulated MPAs. We then calculated the response ratios observed in the PISCO survey data from the Channel Islands, and matched these empirical results with simulations that produced similar response ratios after the same number of years of MPA protection. Because each simulation included measures of both response ratios and population-level effects, this process provides a library of simulations (and their associated attributes) that could have produced the types of empirical response ratios measured in the Channel Islands.

Difference-in-Difference Regression

The DiD analysis used kelp forest survey data from the PISCO surveys in the Channel Islands. 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.1,Fig.2). The details of the monitoring program are described in Caselle et al. (2015). We define the population-level conservation effects of MPAs as the change in mean total biomass densities of targeted fin-fish both inside and outside of MPAs, relative to the mean total biomass densities of targeted fin-fish inside and outside of MPAs that would have occurred without the MPAs.

Building off of Caselle et al. (2015), we used an identification strategy utilizing biomass densities of 11 species that are not directly targeted by fishing as our control group (non-targeted), and biomass densities of 12 species targeted by fishing as our treatment group (Fig.2). Targeted fin-fish species in the Channel Islands available to this study include California sheephead (*Semicossyphus pulcher*), and copper (*Sebastes caurinus*) and blue (*Sebastes mystinus*) rockfish. Non-targeted species include garibaldi (*Hypsypops rubicundus*), halfmoons (*Medialuna californiensis*), and blacksmith (*Chromis punctipinnis*). Our regression estimates 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. To account for the fact that sampling locations are not uniformly distributed across the islands, we weight the samples in our regression in proportion to the total area inside and outside of MPAs in the Channel Islands.

This identification strategy attempts to control for unobserved environmental shocks to the system that are independent of the MPAs. 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. For example, consider an evenly distributed population that has 50% of its range protected by an MPA. If the MPA increases biomass densities inside its boundaries by 20%, and by 0% outside the reserve, the population effect of the MPA estimated by our DiD would be 10%.

The DiD 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.

$$(log(D_{MPA=1,T=1}) - log(D_{MPA=0,T=1})) - (log(D_{MPA=1,T=0}) - log(D_{MPA=0,T=0}))$$

Where *T* indicates targeted species, *MPA* indicates whether MPAs are in place, and *D* is the observed mean total biomass density across all sites.

The simplified form of this regression model is

$$d_i \sim Gamma(e^{\beta_0+\beta_1 T_i+\beta_2 MPA_i+\beta_3 T_i MPA_i+\mathbf{B^c X_i}+\mathbf{B^s S_i}}, shape)$$

$$\mathbf{B^s} \sim Normal(\beta_r, \sigma_r)$$

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. To account for the fact that MPA effects will evolve over time, we estimate a vector of MPA effects in three-year blocks for the all years after the MPAs were implemented in 2003. $\mathbf{B^c}$ is a vector of coefficients for additional control variables in matrix *X* such as water temperature and observer experience. $\mathbf{B^s}$ is a vector of hierarchical coefficients for each sampling location **S** , clustered by island β_r with variance σ_r^2. Under the assumptions of this model, β_3 is the causal effect of the treatment (*MPA*) on the treated (targeted species) (Table.2). We use a Bayesian hierarchical generalized linear model since it allows us to interpret our estimated effects probabilistically (McElreath 2020). Being a Bayesian regression, our DiD analysis produces posterior probability distributions (the probability distribution of our coefficients conditional on the data, priors, and model assumptions) of our coefficients, from which we can construct Bayesian credible intervals (Gelman 2014).

RESULTS

Caselle et al. (2015) found a statistically significant increase in the response ratios of targeted species over time, and evidence that this increase is smaller for non-targeted species. Updating the results of Caselle et al. (2015) using data collected through 2017 shows a continuation of the increasing trend in the response ratios of targeted species (Fig.3). This provides evidence that the

Channel Islands MPAs are large enough and sufficiently well-enforced as to provide meaningful protection within their borders (White et al. 2020).

These response ratios cannot, however, be used as a definitive indicator of population-level effects of these MPAs. In the case of the Channel Islands MPAs, control sites are often located within a few kilometers of an MPA, making them susceptible to both biological spillover and concentration of fishing effort excluded from the MPAs. Our simulation results show that the response ratio trends we observe in the data could plausibly be produced by a wide range of population-level MPA effects (Fig.3). Response ratios well over one were associated with “true” 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 moderate, adult movement is low, larval dispersal is high, and displaced fishing effort concentrates around the border of the MPAs.

Our targeted vs. non-targeted DiD regression provides an alternative approach to spatial controls for estimating population-level MPA effects. 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 31%, 90% credible interval 3% - 69%). 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 79% increase in mean total biomass density of targeted species (90% credible interval 40% - 133%) (Fig.4). These empirical estimates are in line with the outcomes that our simulation model suggests are plausible. However, in the subsequent years the trend reverses itself, and in 2015-2017 we once again see no clear effect of the MPAs (median estimated effect -7%, 90% credible interval -31% - 23%.) (Fig.4).

Our library of simulation results allows us to explore how observation error and natural fish recruitment variation might explain this lack of a clear result in the Channel Islands MPAs. Using a Bayesian DiD regression on these simulated data, we estimated the percent error between the posterior probability distribution of the estimated MPA effect from the regression and the simulated MPA effect. The error in the DiD regression's estimate of the population-level MPA effect was extremely high when MPA effect sizes were less than 25% and the model was faced with both observation and process errors (Fig.5). Even models fit to data generated from large effect sizes commonly mis-estimated 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 "true" population-level MPA effect of at least 30%. In the context of the moderately exploited species in the Channel Islands PISCO data evaluated here, this finding suggests that we should not be surprised at our difficulty in precisely estimating the population-level effect of the MPAs.

Two of the most critical drivers of MPA effect size are the size of the MPA network and the degree of fishing pressure. Looking across these two variables, based on our simulations the MPA network must be large (25% or more of a species' range) and the target species overfished (pre-MPA depletion greater than about 60%) to achieve an effect size with a likely MAPE of 25% or less. Although recently some extremely large MPAs have been enacted that may indeed reach into the higher levels of MPA coverage, most MPA networks for near-shore commercial fin-fish are likely to cover areas more in line with the Channel Islands (20%) or smaller. As such, many MPA networks are expected to have population-level effect sizes that are difficult to detect unless target species were experiencing extreme overfishing prior to MPA establishment, or in the hypothetical world without MPAs (Fig.6-A).

DISCUSSION

Containing a carefully designed, well-enforced, and well-studied MPA network, the Channel Islands seems to be an ideal location to study the population-level effects of protected areas. The targeted vs. non-targeted DiD strategy used here presents an alternative means of estimating the population-level effects of MPAs. Despite having its own strict caveats, this strategy provides some potential improvements over spatial 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 show that under the dynamics of the Channel Islands, particularly given the lack of heavily exploited species such as abalone and deep-water rockfish that helped motivate the Channel Island MPAs in the available data, this result is to be expected. After 14 years of MPA protection we are left without a clear picture of the population-level effect of the Channel Island MPA network on biomass densities of targeted fin-fish.

Fishing dynamics may be one factor contributing to a lack of strong MPA network effects. Much of the theoretical literature on MPAs assumes that larger reserves produce larger conservation gains (White et al. (2011) and references therein). However, these models generally simulate fleet dynamics through fishing mortality rates; the proportion of total mortality experienced by a population attributable to fishing pressure (e.g. Halpern et al. (2004)). Alternatively, under a "constant-catch" strategy, fishers have a catch objective and exert as much (or little) effort as needed to achieve that objective. Subsistence fisheries may use a constant-catch style policy over the short-term, as they seek to ensure that their food needs are met. Constant-catch dynamics might also occur in fisheries with constraining quotas that are not updated after the implementation of MPAs. Fishers pursuing constant-catch in areas outside an MPA may have to fish harder to achieve the same catch from a smaller part of the population, causing a population conservation loss under 70% of our constant-catch simulations. This potential negative interaction between constant-catch and MPAs is an important risk to consider (as done in Little et al. (2011)) especially as MPAs are increasingly implemented in quota-managed fisheries (Liu et al. 2018). 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 (Appendix S1 Fig.S2) which indicates that a negative MPA effect caused by a constant-catch fishing strategy is unlikely.

Another possibility for the estimated decline in Channel Islands MPA effects is environmental disturbance. The Channel Islands region experienced a dramatic 'marine heatwave' beginning in 2014 and persisting through 2016, resulting in part in extremely elevated water temperatures throughout the region (Gentemann et al. 2017). Many of the non-targeted species in the Channel Islands have warm thermal affinities and have increased in numbers since the heatwave (Freedman et al. 2020). The targeted group is made up mostly of fishes with cold-water affinities. 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 fin-fish in the absence of the MPAs, given the magnitude of the environmental shock relative to the size of the population-level MPA effect.

All of the species in this empirical analysis may affect each other through mechanisms such as predation, competition, and habitat modification. We used convergent cross mapping (CCM), in the manner of Clark et al. (2015), to test for significant dynamic interactions between species and therefore the possibility of the trophic cascades biasing our results. We 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 (Appendix S1 Fig.S33-S35). 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.

As the number and size of global MPA networks increase, we must set appropriate expectations for their outcomes on both local and regional scales. Simulation modeling can help inform the range of effect sizes that may be expected, and monitoring programs can 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 (Nickols et al. 2019). 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.

There are many potential alternatives to spatial response ratios for estimating the population effects of MPAs that better account for the challenges of causal inference (though that may be more data-intensive) (Larsen et al. 2019). We applied one such approach here, and yet were still unable to reach robust conclusions as to the effect of MPAs on the total biomass density of targeted fin-fish in the Channel Islands, due to the likely small size of the true effect relative to the influence of environmental variability. There are other promising statistical approaches to setting expectations for MPA effects, including using models fitted to local data to set population-level expectations and create synthetic counterfactuals (White et al. 2011; Nickols et al. 2019).

The scientific communicate must effectively communicate the challenges of estimating the population-level effects of MPAs. Lack of a clear population-level MPA effect should not necessarily be viewed as a failure of a conservation program, and likewise, large response ratios should not be automatically taken as evidence of a population-level conservation success. Rather, results and subsequent management actions 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.

As advocacy for broad networks of MPAs is growing globally, MPA science must directly tackle the challenge of evaluating the performance of MPAs at the population scale. Commonly employed metrics such as spatial response ratios may be applicable in some circumstances, but are vulnerable to inaccuracy or misuse as metrics of population-level effects. 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 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 to ensuring that MPAs play effective roles in fisheries management and marine conservation.

Supporting Information

Detailed descriptions of the simulation model and DiD estimator (Appendix S1) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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TABLES

Table 1: Variables for MPA simulations

Variable	Distribution
Scientific Name	Drawn from all possible species in **`FishLife`** (Thorson et al. (2017))
steepness	uniform(0.6,0.95)
Adult movement ($\sigma_{s=a}$)	uniform(0,0.25 * P)
Larval movement ($\sigma_{s=l}$)	uniform(0,0.25 * P)
Recruitment variation (σ_r)	$\in 0,0.05,.1,.2$
Recruitment autocorrelation (ac_r)	$\in 0,0.05,.1,.2$
Density-dependent adult movement	$\in 0.25,1$
Density-dependence timing	$\in Local, Global, PostDispersal$
% Patches in MPA	uniform(0.01,1)
Initial fishing relative to natural mortality	uniform(0.01,4)
Selectivity as a multiple of maturity length	uniform(0.1,1.25)
Fleet model	$\in OpenAccess, ConstantEffort, ConstantCatch$
Spatial effort model	$\in Uniform, Biomass, Profits$
Years into simulation to start MPA	uniform(5,0.66)
MPA is Larval Source?	$\in TRUE, FALSE$
Randomly place MPA?	$\in TRUE, FALSE$
Fleet reaction to MPA	$\in Concentrate, Leave$
Patchiness	uniform(0.01,0.75)
MPA habitat factor	$\in 1,4$

Table 2: Posterior means and credible interval for key model coefficients. Raw data contained 307264 individual observations, total number of targeted and non-targeted mean mean total biomass densities by site and year used to fit model was 951. Site-level terms omitted for clarity.

Variable	Mean	5th Percentile	95th Percentile
Intercept	-2.81	-3.08	-2.54
Targeted by Fishing	0.06	-0.13	0.25
Year Block (2003,2006]	-0.82	-1.07	-0.55
Year Block (2006,2009]	-0.87	-1.19	-0.52
Year Block (2009,2012]	-0.84	-1.18	-0.49
Year Block (2012,2015]	-0.97	-1.28	-0.61
Year Block (2015,2018]	-0.58	-0.91	-0.21
Observer Experience	0.20	0.05	0.36
(Observer Experience)^2	-0.08	-0.18	0.04
Wave Surge	0.09	0.00	0.17
Kelp Cover	-0.06	-0.11	-0.01
Lagged Commercial Catch	0.06	-0.05	0.17
Water Temperature	0.27	0.07	0.47
Deviation from regional mean temperature	-0.22	-0.40	-0.05
(Deviation from regional mean temperature)^2	0.01	-0.02	0.04
Targeted by Fishing×Year Block (2003,2006]	0.27	0.03	0.53
Targeted by Fishing×Year Block (2006,2009]	0.50	0.25	0.75
Targeted by Fishing×Year Block (2009,2012]	0.58	0.34	0.85
Targeted by Fishing×Year Block (2012,2015]	0.29	0.02	0.56
Targeted by Fishing×Year Block (2015,2018]	-0.08	-0.37	0.20

FIGURES

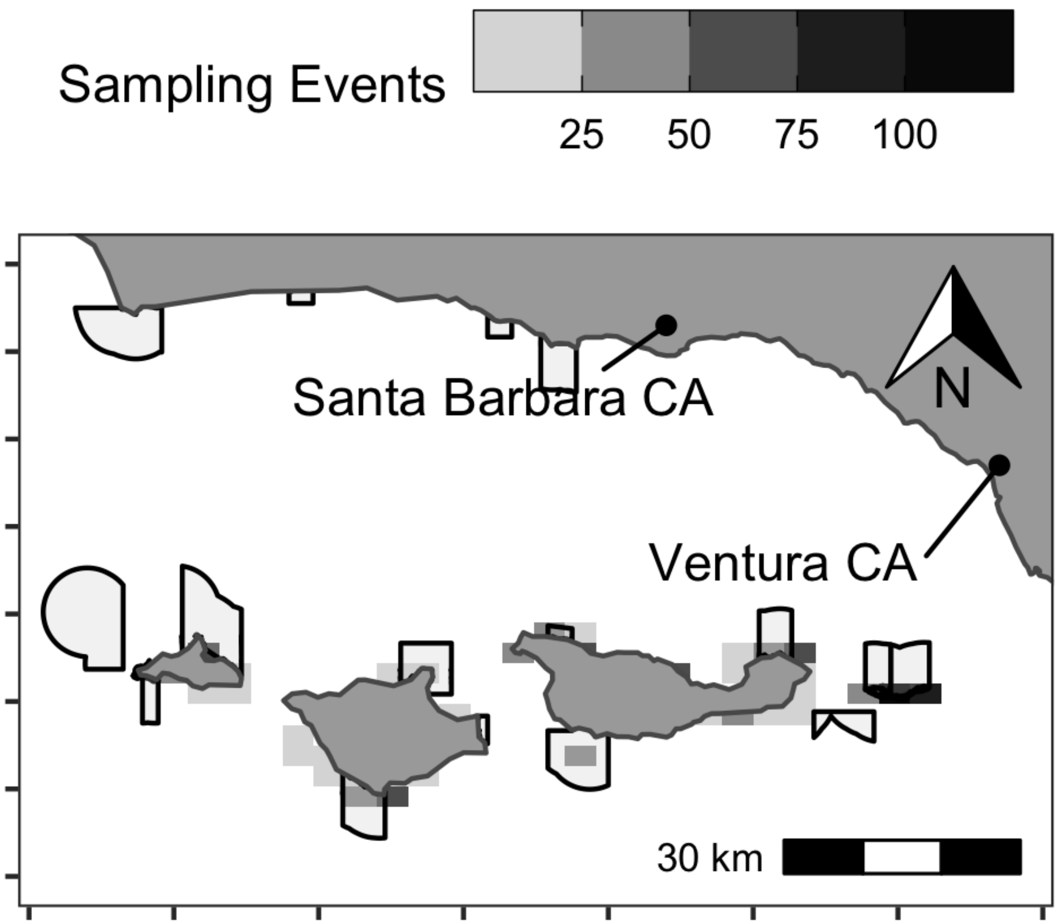

Figure 1: Map of study region; the Northern Channel Islands, California, USA. Shading shows binned number of PISCO sampling events across the time period of our study.

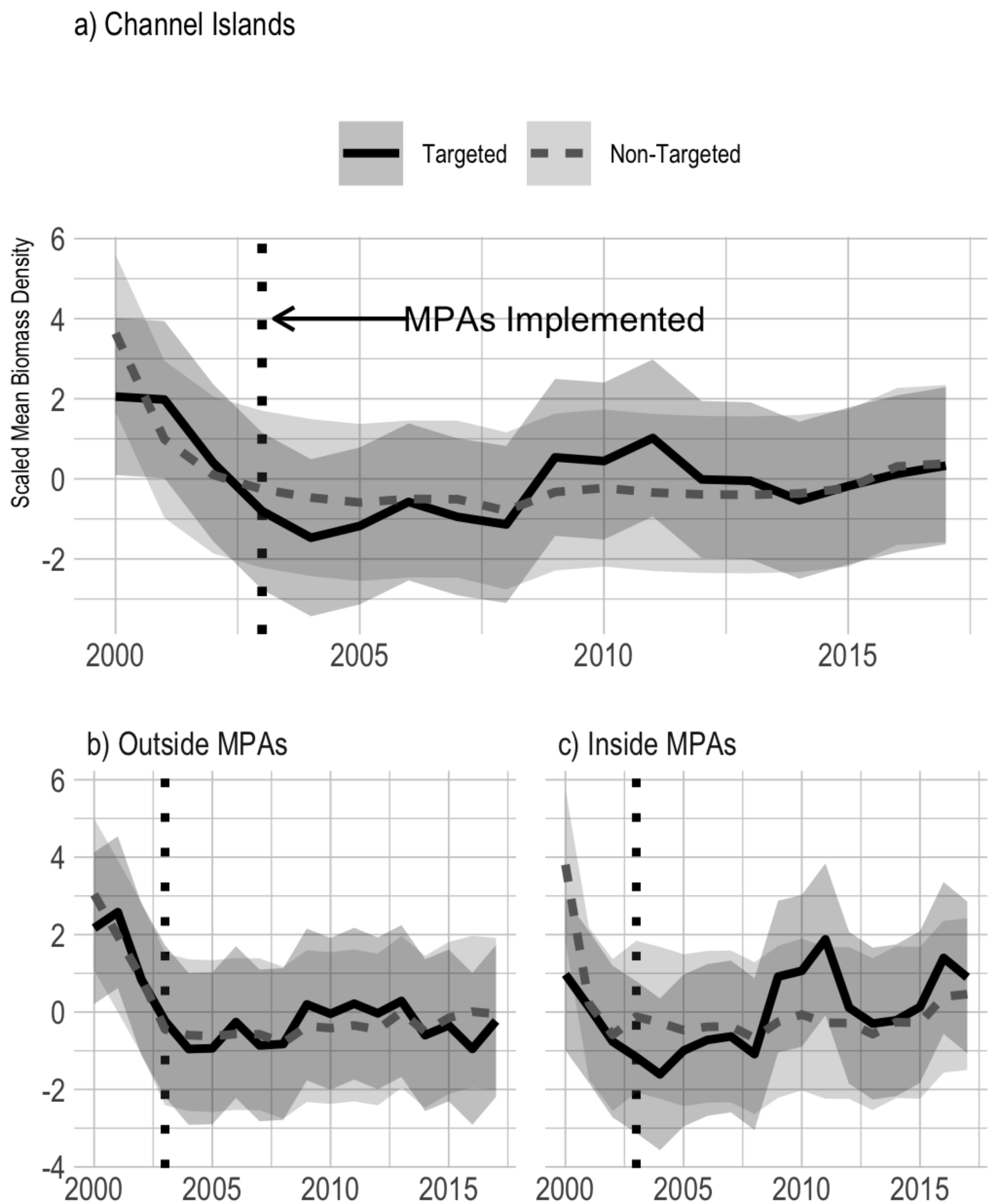

Figure 2: Centered and scaled trends in biomass densities of targeted and non-targeted fin-fish included in our study. Panel a) shows mean trends across all sites, with shaded areas shwoing 95% confidence intervals. Bottom two panels show same trends but only including sites b) outside and c) inside MPAs

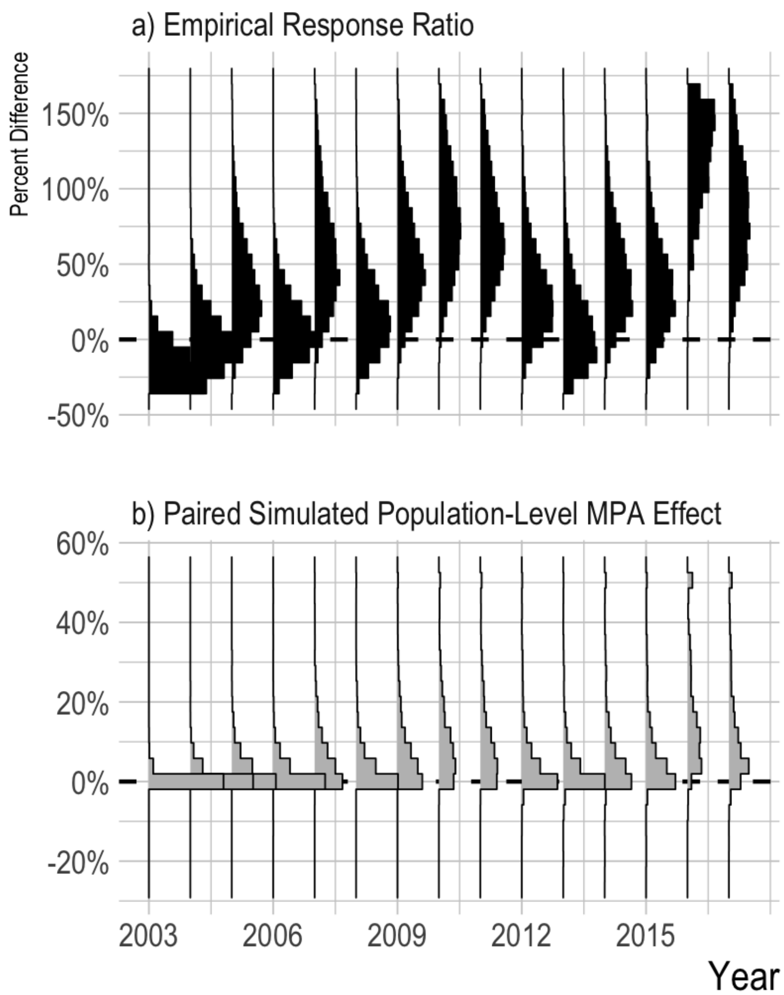

Figure 3: Simulated population effects (panel *a* in grey) that could have produced observed response ratios (panel *b*) in black) in the Channel Islands. Panel *a*) histograms show 90% posterior probability distributions of response ratios for targeted species (x-axis) over time (y-axis). Panel b) Simulated population-level (pop.) effect on biomass densities matched to empirical response ratios in a). For response ratios, a percent difference value of zero indicates that biomass densities of targeted species are identical inside and outside MPAs, a percent difference value of one that biomass densities of targeted species are 100% greater inside MPAs relative to outside. For MPA population effect, a percent difference value of zero indicates that biomass densities are identical in the with- and without- MPA scenarios. A percent difference value of one indicates that biomass densities are 100% greater in the scenario with MPAs than the scenario without MPAs.

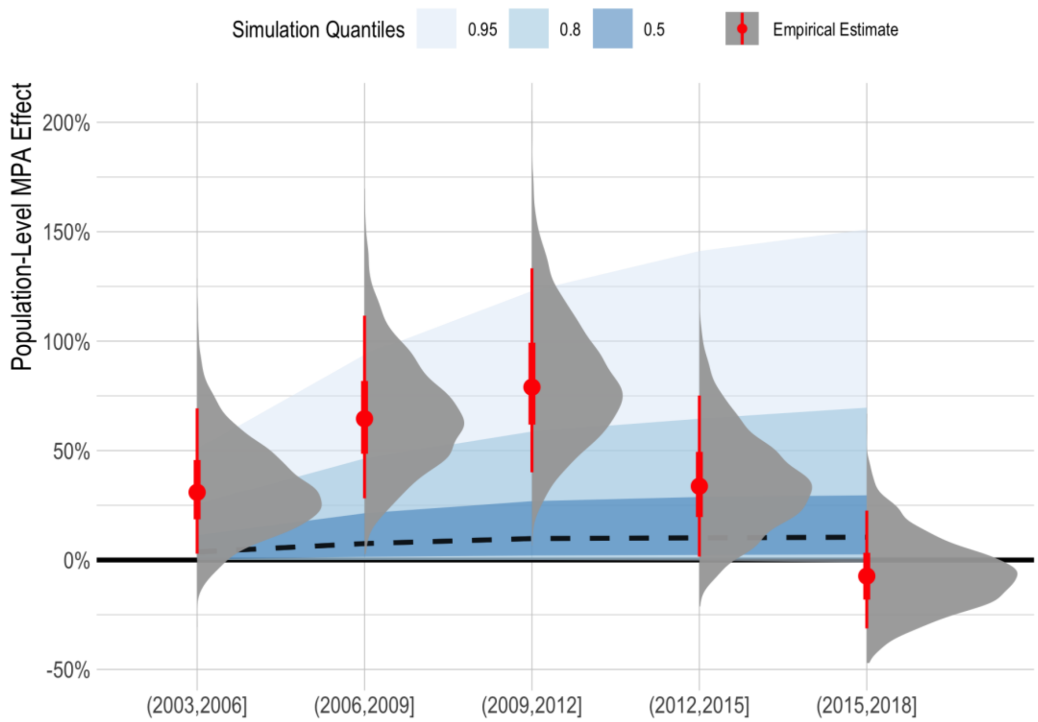

Figure 4: Results of Difference-in-Difference regression estimating the population-level effect of the Channel Island MPAs on mean total biomass densities of targeted species. Grey distributions show posterior probability distribution of estimated MPA effect; red point is median estimated effect, thicker 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. MPAs were implemented in 2003.

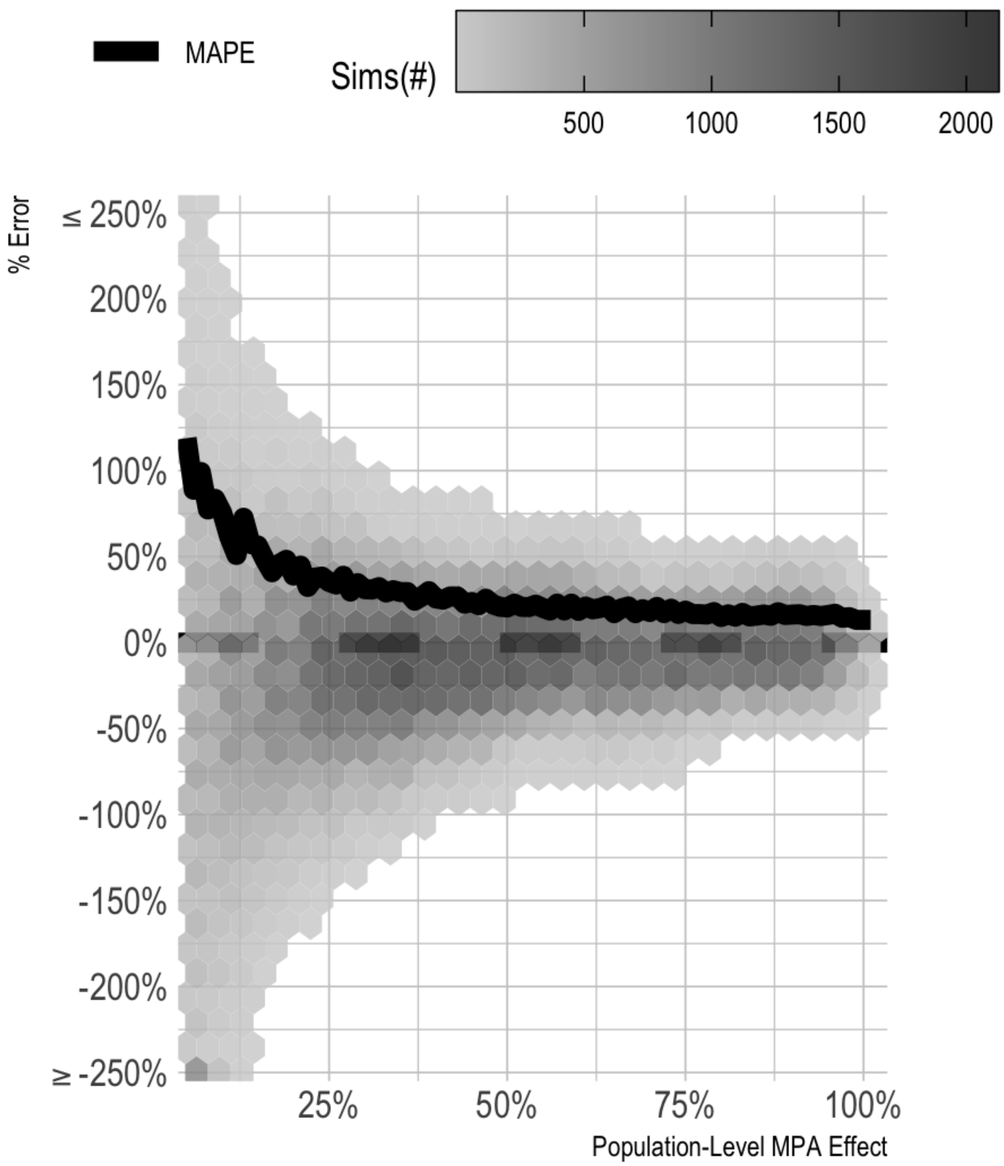

Figure 5: Distribution of percent error in posterior estimates of population-level MPA effect (y-axis) plotted against true simulated MPA effect (x-axis). Shading shows concentration of simulations. Black line shows mean absolute percent error (MAPE) as a function of simulated population-level MPA effect.

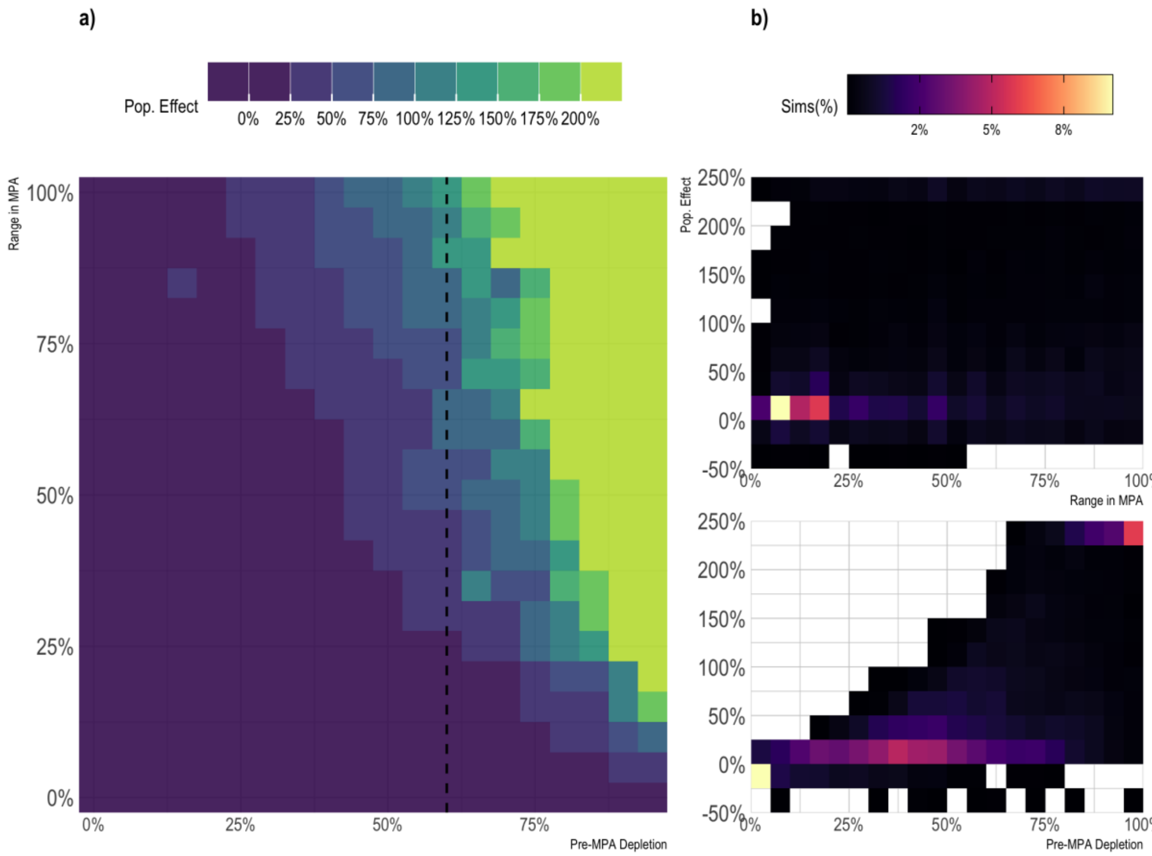

Figure 6: Simulated population-level effects of MPAs. Panel a) shows median simulated population-level (pop.) MPA effect sizes as a function of percent of species' range inside MPA (x-axis), and pre-MPA depletion (y-axis). Pre-MPA depletion is a measure of fishing pressure, where 0 means that the population is unfished, and 1 means that the population is extinct in the time period immediately prior to MPA implementation. Panel b) shows distribution of simulations across range of MPA size and pre-MPA depletion separately.