Conservation Biology

Assessing the population-level conservation effects of marine protected areas

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Article impact statement: Population-level conservation effects of marine protected areas are likely to be extremely challenging to measure and detect.

Abstract

Marine protected areas (MPAs) cover 3–7% of the world's ocean, and international organizations call for 30% coverage by 2030. Although 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 connected populations that span beyond their borders. A network of MPAs covering roughly 20% of the Channel Islands National Marine Sanctuary was established in 2003, with a goal of providing regional conservation and fishery benefits. We used a spatially explicit bioeconomic simulation model and a Bayesian difference-in-difference regression to examine the conditions under which MPAs can provide population-level conservation benefits inside and outside their borders and to assess evidence of those benefits in the Channel Islands. As of 2017, we estimated that biomass densities of targeted fin-fish had a median value 81% higher (90% credible interval: 23–148) inside the Channel Island MPAs than outside. However, we found no clear effect of these MPAs on mean total biomass densities at the population level: estimated median effect was –7% (90% credible interval: –31 to 23) from 2015 to 2017. Our simulation model showed that effect sizes of MPAs of <30% were likely to be difficult to detect (even when they were present); smaller effect sizes (which are likely to be common) were even harder to detect. Clearly, communicating expectations and uncertainties around MPAs is critical to ensuring that MPAs are effective. We provide a novel assessment of the population-level effects of a large MPA network across many different species of targeted fin-fish, and our results offer guidance for communities charged with monitoring and adapting MPAs.

KEYWORDS
bioeconomic modeling, causal inference, Channel Islands National Marine Sanctuary, marine conservation, marine protected area networks, program evaluation

Resumen

Las áreas marinas protegidas (AMPs) cubren entre 3–7% de los océanos del planeta y las organizaciones internacionales piden una cobertura del 30% para el 2030. Aunque numerosos estudios muestran que las AMPs producen beneficios de conservación dentro de sus límites, muchas de estas áreas también están justificadas por otorgarles beneficios de conservación a las poblaciones conectadas que abarcan más allá de sus fronteras. Una red de AMPs que cubre aproximadamente el 20% del Santuario Marino Nacional de las Islas del Canal fue establecida en 2003 con el objetivo de proporcionar beneficios para la conservación y las pesquerías regionales. Usamos un modelo de simulación bioeconómica

espacialmente explícito y una regresión bayesiana de diferencia-en-diferencia para examinar las condiciones bajo las que las AMPs pueden proporcionar beneficios de conservación a nivel poblacional dentro y fuera de sus límites y para evaluar las evidencias de esos beneficios en las Islas del Canal. Hasta el 2017, estimamos que la densidad de la biomasa de los peces focalizados tuvo un valor medio de 81% (90% intervalo creíble 23–148) dentro de las AMPs de las Islas del Canal que fuera de ellas. Sin embargo, no encontramos un efecto claro de estas AMPs sobre la densidad de biomasa total promedio a nivel poblacional; el efecto medio estimado fue de -7% (90% intervalo creíble -31 - 23) entre 2015 y 2017. Nuestro modelo de simulación mostró que los tamaños del efecto de las AMPs menores al 30% tenían mayor probabilidad de ser difíciles de detectar (incluso cuando estaban presentes); los tamaños de efecto más pequeños (que es probable que sean comunes) fueron incluso más difíciles de detectar. Claramente, es muy importante comunicar las expectativas e incertidumbres en torno a las AMPs para asegurar que éstas sean efectivas. Proporcionamos una evaluación novedosa de los efectos a nivel poblacional de una red extensa de AMPs para muchas especies de peces focalizados y nuestros resultados ofrecen una guía para las comunidades encargadas de monitorear y adaptar las AMPs.

PALABRAS CLAVE
conservación marina, inferencia causal, modelo bioeconómico, programa de evaluación, redes de áreas marinas protegidas, Santuario Marino Nacional de las Islas del Canal

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 largely 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 local and regional population-level effects. Numerous factors influence the population-level effects of MPAs. These include the scale of adult and larval dispersal relative to the size of the MPAs (Gaines et al., 2003); strength, timing, and location of density dependence (Burgess et al., 2014); design of the network (Gaines et al., 2010; Rassweiler et al., 2014); degree of enforcement (Edgar et al., 2014); level of fishing pressure; 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 MPAs. In contrast to this population paradigm used in MPA simulations, MPAs are often evaluated empirically at local scales with 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 MPAs (Halpern, 2003; Lester et al., 2009; Edgar et al., 2014; Caselle et al., 2015). These studies show clear evidence that well-enforced and sufficiently sized MPAs are associated with high response ratios. Several studies document 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 show similarly clear and positive results (Thiault et al., 2019). These studies demonstrate the ability of MPAs to create differences between local fished and unfished areas.

What is lacking is clear evidence for the population-level effects of MPAs. Spatial inside-versus-outside studies rely on an assumption that selected control sites serve as a measure of what would have happened in the absence of MPAs. Habitat characteristics are often used to justify the selection of particular fished sites as counterfactuals (controls) in response ratios (Ferraro et al., 2019). However, beyond habitat differences, the very spillover effects it is hoped MPAs produce can negate the ability of spatial response ratio or BACI designs to accurately estimate the effects of MPAs because these methods require that control sites be conditionally unaffected by the treatment (Moffitt et al., 2013; Ferraro et al., 2019). Spillover of adults or larvae from MPAs to control sites can mask conservation benefits, whereas displacement of fishing effort from MPAs to control sites (which is rarely addressed directly

[Ferraro et al., 2019]) can lead to overestimates of conservation gains caused by MPAs measured by spatial response ratios. 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. Because variations of spatial response ratios and BACI studies have been a primary source of evidence for the conservation effects of MPAs, this means empirical understanding of the population-level impacts of MPAs is surprisingly limited.

We conducted a paired theoretical and empirical assessment to examine the challenges of assessing population-level impacts of MPAs. In 2003, a network of MPAs was established in the Channel Islands National Marine Sanctuary, California (USA) (hereafter Channel Islands). This MPA network covers approximately 20% of the Channel Islands' waters (which span over 800 km^2). The network has been used as a model in protected area design around the world (Botsford et al., 2014). We used data from the first 14 years of protection in a difference-in-difference (DiD) model (Angrist & Pischke, 2009) to assess the population-level effect of a large MPA network on a wide array of fin-fish species. Rather than relying on spatial controls, we used groups of species targeted and not targeted by fishing pressure as our treatment and control groups. We built on existing MPA theory to interpret our results and devised guidance for scientists and managers as to when and how they might expect to detect population-level conservation effects of MPAs.

METHODS

We built a spatially explicit bioeconomic simulation model and conducted a Bayesian DiD regression. The DiD is akin to a BACI in that it is used to assess changes in control and treatment groups before and after treatment (Larsen et al., 2019). We used our bioeconomic simulation model to provide theoretical expectations of population-level effects of MPAs, which we then compared with the empirical results from our DiD regression.

All analyses were conducted in R (R Core Team, 2019). Our DiD regression was fit with Stan (Carpenter et al., 2017) through the rstanarm package (Goodrich et al., 2020). All data and code needed to fully replicate our study are publicly available from github.com/DanOvando/population-effects-of-mpas. Detailed descriptions of the simulation model structure and sensitivity analyses of our estimation model are in Appendix S2.

Simulation model

Our bioeconomic model simulated the effect of MPAs on a spatially explicit age-structured representation of a fish population. Readers can explore the functionality of the model with the online tool available from danovando.shinyapps.io/simmpa/. The purpose of the simulation model was to set expectations

for our empirical results and 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 and the equations of the simulation model are in Appendix S2. We used this model to generate 10,168 simulated MPA outcomes across 7618 species.

Many authors 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 authors into a cohesive model, similar in spirit to Krueck et al. (2017). The simulation model consisted of 50 patches with wrapped edges. For each simulation, we first randomly pulled a species and its associated life-history traits from the FishLife (Thorson et al., 2017) package. We paired these data with randomly selected values governing the characteristics of the simulation (Appendix S2). Key choices available to the model include parameters governing fishing pressure and MPA design. For a given simulation, the model randomly selected a fleet model and fishing effort allocation strategy. The fleet model could be either constant catch (fleet exerts as much effort as needed to maintain a fixed amount of catch), constant effort (fleet maintains a constant amount of effort over time), or open access (fishing effort of fleet expands and contracts in response to available profits). The total fishing effort exerted by the fleet was then distributed in space uniformly, in proportion to spatial catch per unit effort or in proportion to spatial profit per unit effort.

The simulation then applied the fleet model to the population, and in a randomly selected year implemented an MPA network. The model sampled a percentage of the population's range to place in MPAs, and randomly assigned patches to MPAs either across a uniform system or preferentially on higher quality habitat. The model then randomly selected whether fishing effort that used to operate inside the MPAs was redistributed to areas outside the MPAs or left the fishery entirely. We then continued the simulations with the MPAs in place. Each simulation was paired with a simulation identical in every way except that MPAs were not implemented (i.e., a simulated control). Using these paired simulations, we calculated the effect of the MPAs on the population as the difference between biomass densities in the simulation with MPAs and biomass densities in the simulation without MPAs.

These simulation results provided 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), which provided the data from the Channel Islands that we used in this study. For this set, we only included species of the same genus as those targeted by fishing in the PISCO data. We also restricted fishing pressure such that the simulated populations were moderately to lightly exploited (because the PISCO data we used exclude deeper water species, such as boccacio [*Sebastes paucispinis*], which were overexploited at the inception of the MPAs, and threatened invertebrates, such as red abalone [*Haliotis rufescens*]), and capped the MPA size at 20% of the population's range (Rassweiler et al., 2012). For each of these Channel Islands
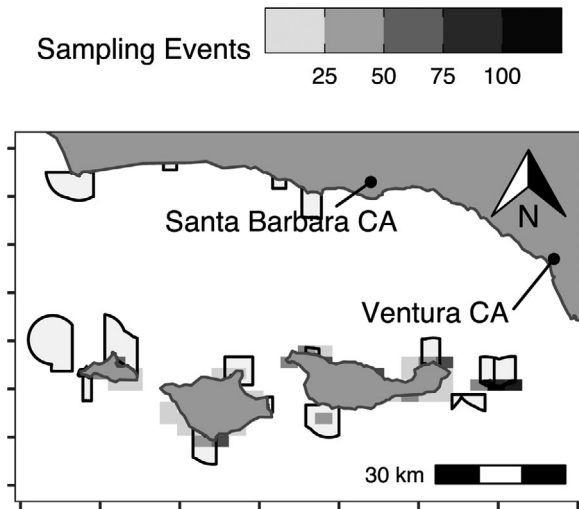
FIGURE 1 Map of the study region in the Northern Channel Islands, California (USA) (shading, binned number of Partnership for Interdisciplinary Studies of Coastal Oceans [PISCO] sampling events over the study period)

simulations, we calculated the true population-wide difference in biomass between the simulations with and without the MPAs and 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 provided 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

We used kelp forest survey data from the PISCO surveys in the Channel Islands in the DiD analyses. Divers from PISCO conducted visual scuba surveys at a large number of rocky reef and kelp forest sites inside and outside MPAs throughout the Channel Islands to produce estimates of densities of fishes that are both targeted and nontargeted by fishers (Figures 1 and 2). The details of the monitoring program are described in Caselle et al. (2015). We defined the population-level conservation effects of MPAs as the change in mean total biomass densities of targeted fin-fish inside and outside MPAs relative to the mean total biomass densities of targeted fin-fish inside and outside MPAs that would have occurred without the MPAs.

Building on Caselle et al. (2015), we used an identification strategy in which 11 species not directly targeted by fishing comprised the control group (nontargeted) and 12 species targeted by fishing comprised the treatment group (Figure 2). We then measured differences between the trends of biomass densities of the treated group relative to the trends we would have expected based on the biomass densities of the control group. Data on targeted fin-fish species in the Channel Islands available

to this study included California sheephead (*Semicossyphus pulcher*) and copper (*Sebastes caurinus*) and blue rockfish (*Sebastes mystinus*). Nontargeted species included garibaldi (*Hypsypops rubicundus*), halfmoons (*Medialuna californiensis*), and blacksmith (*Chromis punctipinnis*). Our regression estimated 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 were not uniformly distributed across the islands, we weighted the samples in our regression in proportion to the total area inside and outside the MPAs.

This identification strategy attempted to control for unobserved environmental shocks to the system that are independent of the MPAs. Conditional on the assumptions of the model, this regression produced 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 increased biomass densities by 20% insides its boundaries, but had a 0% effect on the connected population outside its boundaries, the population effect of the MPA estimated by our DiD would be 10%.

The DiD regression amounts to estimating the pre- and post-MPA difference in the biomass densities of targeted species, minus the same difference for nontargeted species in the Channel Islands:

$$\left[\log\left(D_{\mathrm{MPA}=1,T=1}\right) - \log\left(D_{\mathrm{MPA}=0,T=1}\right)\right]$$
$$- \left[\log\left(D_{\mathrm{MPA}=1,T=0}\right) - \log\left(D_{\mathrm{MPA}=0,T=0}\right)\right]) \tag{1}$$

where T is targeted ($T = 1$) or nontargeted ($T = 0$) by fishing, MPA indicates whether the data are pre-MPA (0) or post-MPA (1), and D is the observed mean total biomass density across all observations of the appropriate group.

The expanded DiD regression is

$$d_i \sim Gamma\left(e^{\beta_0+\beta_1 T_i+\beta_2 \mathrm{MPA}_i+\beta_3 T_i \mathrm{MPA}_i+\mathbf{B}^c \mathbf{X}_i+\mathbf{B}^s S_i}, \mathrm{shape}\right)$$
$$\mathbf{B}^s \sim Normal\left(\beta_r, \sigma_r\right) \tag{2}$$

where d_i is the biomass density at observation i. To account for the fact that MPA effects evolve over time, we estimated a vector of MPA effects in 3-year blocks for all years after the MPAs were implemented in 2003. The $\mathbf{B}^c$ is a vector of coefficients for additional control variables in matrix $\mathbf{X}$, such as water temperature and observer experience, and $\mathbf{B}^s$ 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 = 1) on the treated targeted group ($T = 1$) (Appendix S4). We used a Bayesian hierarchical generalized linear model because it allowed us to interpret our estimated effects probabilistically. Being a Bayesian regression, our DiD analysis produced posterior probability distributions (the probability distribution of our coefficients conditional on the data, priors, and model assumptions) of our
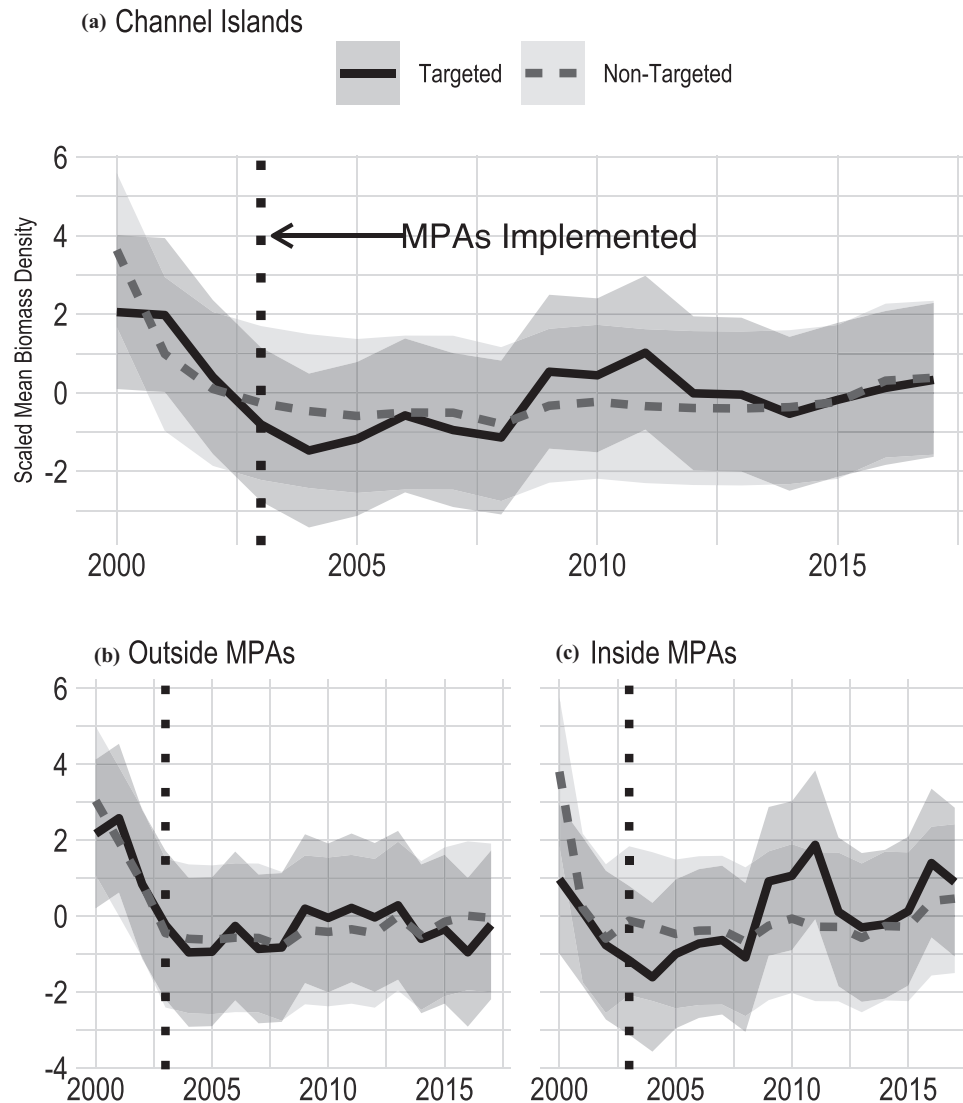
FIGURE 2 Centered and scaled trends in biomass densities of targeted (solid lines) and nontargeted (dashed lines) fin-fish included in our study of the Channel Islands Marine Protected Area (MPA) network: (a) mean trends across all sites and the same trends for sites only (b) outside and (c) inside MPAs (shaded areas, 95% confidence intervals; vertical dotted line, MPA implementation in 2003)

coefficients, from which we constructed Bayesian credible intervals (also termed *uncertainty* or *compatibility* intervals) (Gelman, 2014; McElreath, 2020).

## Simulating difference-in-difference performance

Our library of simulation results allowed us to explore how accurate estimates of population-level MPA effects generated by a DiD regression in the style used here are likely to be under a plausible set of scenarios. We fitted a simplified DiD regression to data generated from simulation results that spanned a range of observation error and degrees of autocorrelated recruitment variation and allowed for potentially negatively correlated recruitment shocks between targeted and nontargeted species. We then estimated the percent error between the posterior probability distribution of the estimated MPA effect from the regression and the true simulated MPA effect and examined how the error in the DiD estimate changed as a function of the true simulated MPA effect.

RESULTS

Updating the results of Caselle et al. (2015) with data collected through 2017, we found an increasing but fluctuating trend in the empirical response ratios of targeted species (Figure 3). We then compared these empirical response ratios to the population-level effects generated by simulated MPAs that had simulated response ratios similar to those observed in the data.

Simulations of the Channel Island MPAs that produced response ratios over 50% had a median simulated population-level effect on total biomass of 2.5% (90% of which fell between 0% and 24%). This means that in the majority of simulations, response ratios >50% were produced by population-level

(a) Empirical Response Ratio

(b) Paired Simulated Population-Level MPA Effect
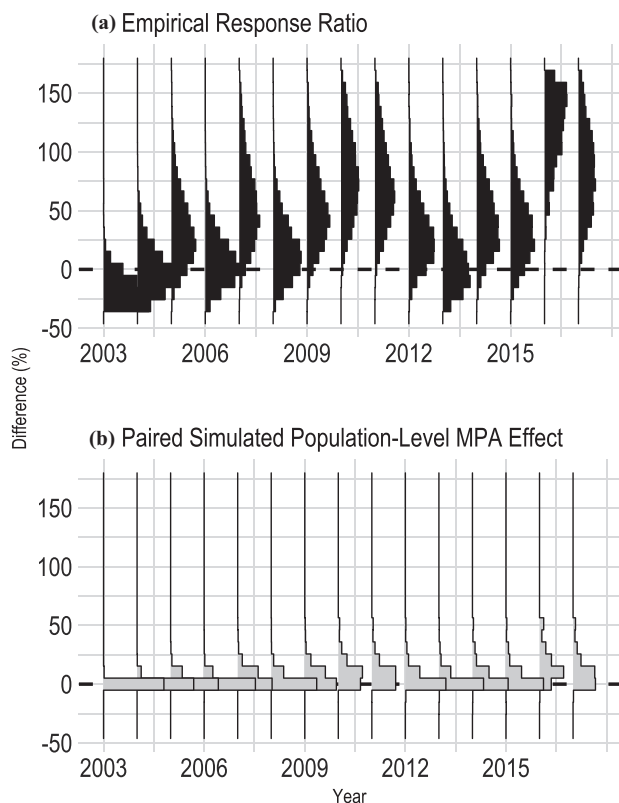
FIGURE 3 For the Channel Islands Marine Protected Area (MPA), (a) empirically observed 90% posterior probability distributions of response ratios of biomass densities inside MPAs relative to biomass densities outside MPAs (0%, biomass densities of targeted species identical inside and outside MPAs; 100%, biomass densities 100% greater inside MPAs than outside) and (b) simulated population-level effects on biomass densities of fin-fish matched to empirical response ratios that could have produced observed response ratios in (a) (0% difference, biomass densities are identical in the with- and without-MPA scenarios; 100% difference, biomass densities are 100% greater in the scenario with MPAs than the scenario without)

effects of <10%, measured as a percent gain in total population biomass inside and outside MPAs.

Over the first 3 years of implementation (2003–2006), the effects of the MPAs were unclear. The median estimated population-level effect over this period was 31%. There was statistical support for a small (3%, bottom 5th percentile of the posterior probability distribution) to large (>69%, top 95th percentile of the posterior probability distribution) effect.

From 2006 to 2012, the model estimated greater probabilities of an increasingly positive MPA effect that peaked in 2009–2011. The median estimate of the population-level MPA effect in this period was a 79% increase in mean total biomass density of targeted species (90% credible interval, 40–133) (Figure 4). These estimates were in line with outcomes our simulation model suggested were plausible. However, in the subsequent years the trend reversed, and in 2015–2017 there was once again no clear effect of the MPAs (median estimated effect, −7%; 90% credible interval, −31 to 23) (Figure 4).

Turning to our assessment of the ability of the kind of DiD model employed here to detect the true population-level effect of an MPA network, the percent error in the DiD regression's

estimate of the population-level MPA effect was extremely high when MPA effect sizes were <25%, and the model had both observation and process errors in the simulated data (Figure 5). Even models fitted 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 data sets required a true population-level MPA effect of at least 30%.

Two of the most critical drivers of MPA effect size were the size of the MPA network and the degree of fishing pressure (Figure 6). Based on our simulations, the MPA network had to be large (25% or more of a species' range) and the target species overfished (pre-MPA depletion >60%) to achieve an effect size with a likely MAPE of 25% or less (Figures 5 and 6).

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. But, in contrast to clear differences in biomass densities observed inside and outside well-protected MPAs, both globally (Lester et al., 2009) and in the Channel Islands (Caselle et al., 2015) we were unable to detect a clear population effect from the Channel Islands MPAs.

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 nontargeted species. We found a similar increasing trend in the response ratios of targeted species (Figure 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 were 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. According to our simulations, the response ratio trends we observe in the data could plausibly be produced by a wide range of population-level MPA effects, the majority of which were <10% (Figure 3). 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 versus nontargeted DiD regression provides an alternative approach to spatial controls for estimating population-level MPA effects that does not rely on the assumption that MPAs do not affect control sites, a required assumption of spatial response ratios. Although we estimated an uncertain but overall positive effect of the MPA network in its first few years of existence, we were unable to detect a robust signal from 2012 to 2017. We found that given the dynamics of the Channel Islands, particularly given the lack of heavily exploited species (e.g., abalone and deep-water rockfish), that helped motivate the Channel Island MPAs in the available data, this result was to be expected. After 14 years of MPA
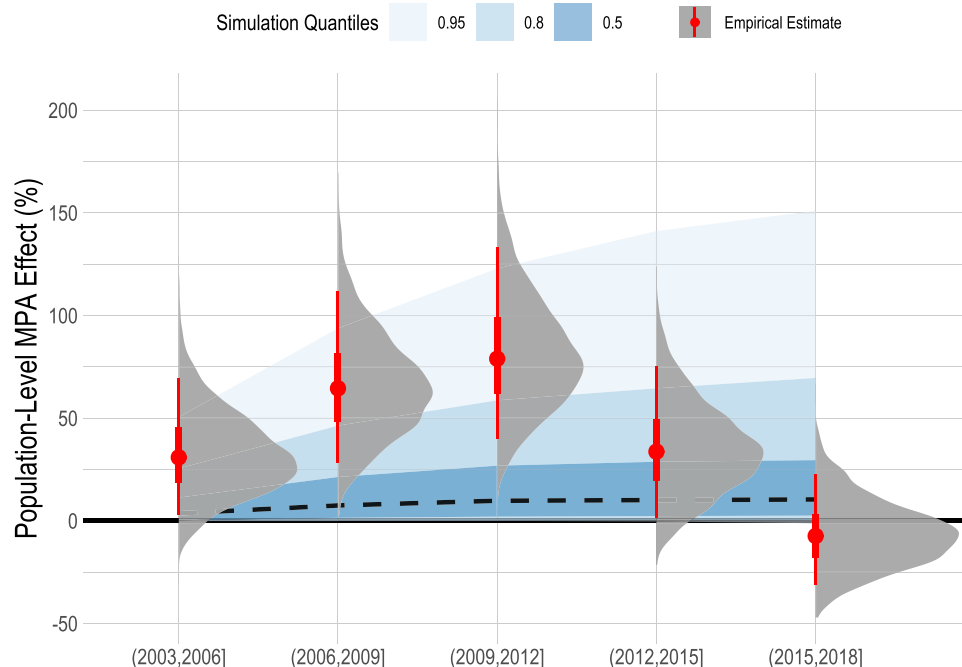
FIGURE 4 Results of difference-in-difference regression estimating the population-level effect of the Channel Island Marine Protect Area (MPA) on mean total biomass densities of targeted species. Gray distributions show posterior probability distribution of estimated MPA effect; red point is median estimated effect, thicker red line 50% credible interval, and 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 3 years, with notation of (2003,2006] indicating that that block includes years ≥2003 and <2006. MPAs were implemented in 2003
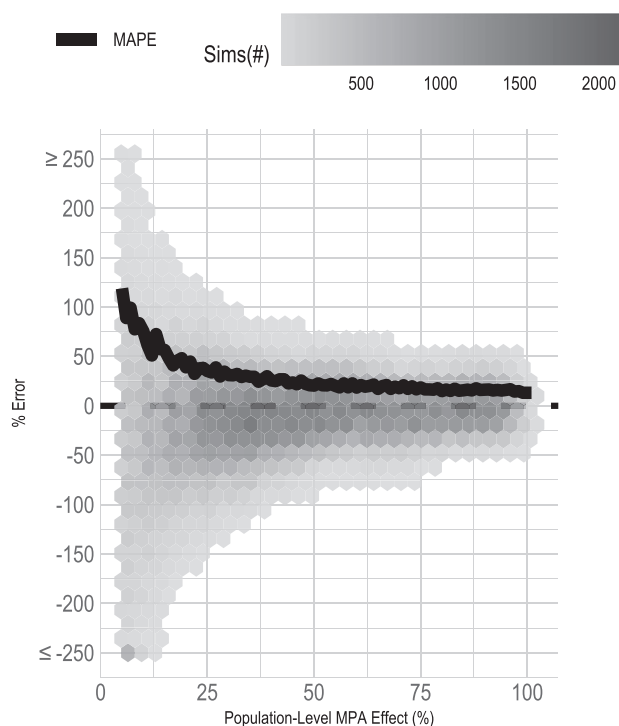
FIGURE 5 Distribution of percent error (y-axis) in posterior estimates of population-level marine protected area effect relative to true simulated MPA effect (x-axis). Shading shows concentration of simulations. Black line shows mean absolute percent error (MAPE) as a function of simulated population-level MPA effect

protection, there is no 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 is based on the assumption that larger reserves produce larger conservation gains (White et al., 2011). However, these models generally simulate fleet dynamics through fishing mortality rates; that is, 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 fishers may use a constant-catch style policy over the short term if they seek to ensure that 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 a constant-catch strategy 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 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 because MPAs are increasingly implemented in quota-managed fisheries (Liu et al., 2018). We did not have access to fine-scale fishing data from the Channel Islands alone, but reported catches for the species of interest in the Santa Barbara region exhibited a mix of stable, downward, and upward trajectories (Appendix S3), which
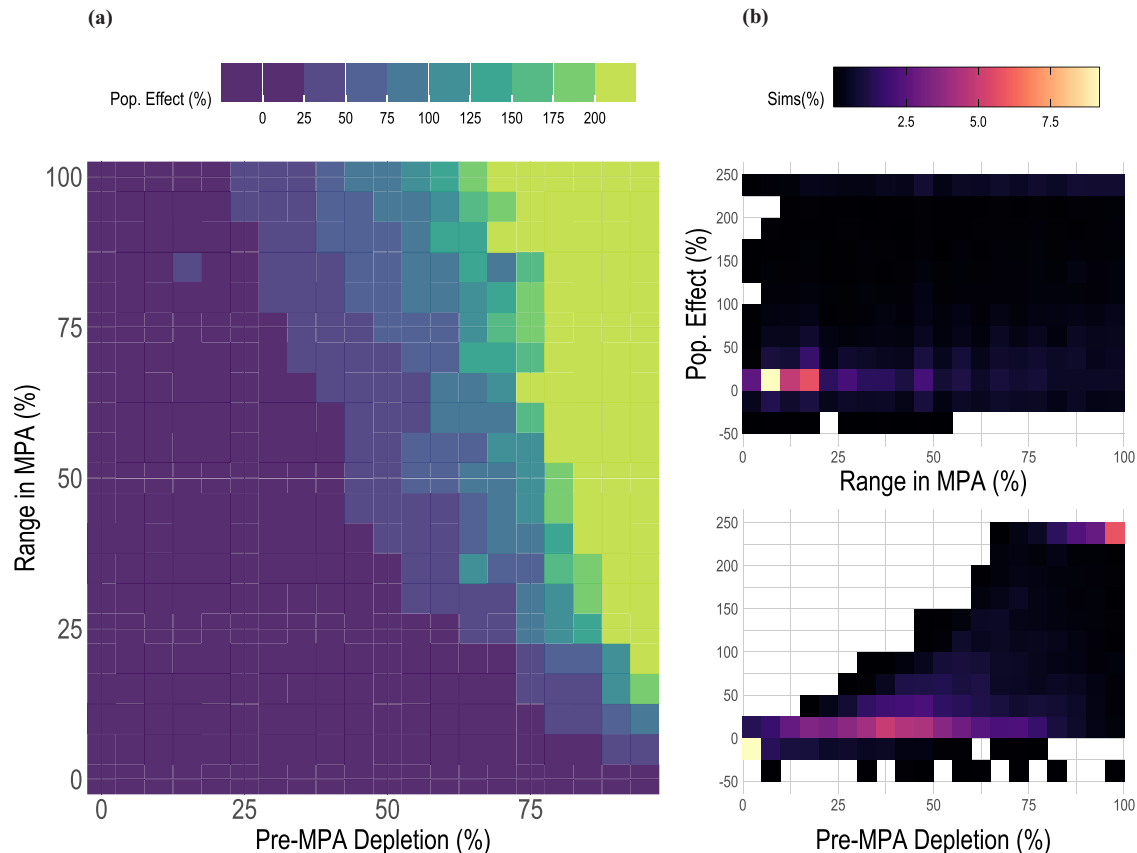
FIGURE 6 Simulated population-level effects of marine protected areas (MPAs). (a) Median simulated fin-fish population-level (pop.) MPA effect sizes (percent change in total biomass) as a function of percentage of species' range inside MPA (*y*-axis) and pre-MPA depletion (*x*-axis). Pre-MPA depletion is a measure of fishing pressure, where 0% means the population is unfished and 100% means the population is extinct in the period immediately prior to MPA implementation. (b) Distribution of simulations across range of MPA sizes and pre-MPA depletions, shown separately

indicates that a negative MPA effect caused by a constant-catch fishing strategy is unlikely.

Environmental disturbance is another possible explanation for the decline in the population-level effects of Channel Islands MPA estimated by our model. 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 nontargeted 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 nontargeted 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 nontargeted species, indicating that although clearly there were interactions between these groups on some level, the effects within the time span of the data were not pronounced enough to affect our results (Appendix S7). However, the longer MPAs are in place, the greater the possibility that substantial species interactions that can affect use of nontargeted 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 spatiotemporal 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, yet we 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. In the context of the moderately exploited species in the Channel Islands PISCO data, our simulation testing suggests that we should not have been surprised at our difficulty in precisely estimating the population-level effect of the MPAs. 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 community 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. 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 the target species would have been extremely overfished without the protection of MPAs (Figure 6a).

As advocacy for large networks of MPAs grows around the world, MPA scientists 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. Bioeconomic 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 to expect from and what can be detected from MPAs is critical to ensuring that MPAs play effective roles in fisheries management and marine conservation.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.