Assessing the Population-level Conservation Effects of Marine Protected Areas

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. 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. We show that MPA effect sizes less than 30% are likely to be difficult to detect (even when they are present); 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-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. Traditional cultures in Oceania utilized - often temporary - MPAs as “fish banks” for times of need (Johannes 1978). Modern MPAs were first established as marine analogs to the terrestrial protection of iconic landscapes (IUCN 1976). Over time our goals and expectations for MPAs have evolved and become more ambitious. Recent international agreements to expand MPAs are based on the assumption that well-designed MPAs will achieve benefits both within, and outside, their borders (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; Gerber et al. 2005; Edgar et al. 2014). As conservation benefits accrue inside MPAs, 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 result in MPAs affecting not only the organisms within their borders, but the broader connected population of affected species. Theory states that numerous factors influence how MPAs might affect fish populations. These include the scale of adult and larval dispersal relative to the size of the MPAs (Gaines et al. 2003; Gerber et al. 2005; Botsford et al. 2008; McGilliard & Hilborn 2008; Di Franco et al. 2018), the strength, timing, and location of density dependence (Burgess et al. 2014), the degree of enforcement (Edgar et al. 2014), how overfished the population would be without the MPA, the time span under evaluation, and how fishing and management responds to the implementation of the MPAs (Hilborn et al. 2004; White et al. 2010, 2011, Moffitt et al. 2013; Walters et al. 2000; Botsford et al. 2003; Gerber et al. 2003; Hastings & Botsford 2003; Smith & Wilen 2003; Smith et al. 2006; Gaines et al. 2010; Ovando et al. 2016). The location and spacing of the MPAs within a network can also influence population-level impacts through network effects (Costello et al. 2010; Gaines et al. 2010).

What empirical evidence is there for these population-level effects of MPAs? Conservation outcomes of MPAs are generally evaluated by “response ratios”, commonly measured as the ratio of biomass densities of species inside relative to outside of MPAs (Lester et al. 2009; Caselle et al. 2015; Halpern 2003; Edgar et al. 2014). 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 (Baetscher et al. 2019; Russ & Alcala 1996; McClanahan & Mangi 2000; Stobart et al. 2009; Pelc et al. 2009; Halpern et al. 2009; Kay et al. 2012; Thompson et al. 2017). MPAs have also caused alterations in fishing effort (Murawski et al. 2005; Mason et al. 2012; Costa et al. 2013; McDermott et al. 2019). Why does this large body of empirical work not serve as sufficient evidence for the population-level effects of MPAs?

Spillover-based studies provide evidence that MPAs may have effects outside their borders, but they are not sufficient evidence for the population effect of MPAs. Response ratios have shortcomings as measures of population-level effects as well. Control sites used in calculating response ratios are often selected based on habitat characteristics (Ferraro et al. 2018). However, export of adults or larvae from the MPA to these “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 is challenging. Response ratios can be a highly imprecise and biased measure of the population-level conservation effect of an MPA network (Moffitt et al. 2013; Ferraro et al. 2018). As response ratios are our primary source of evidence for the conservation effects of MPAs, this means that our collective understanding of the population-level impacts of MPAs is surprisingly limited.

The MPAs within the Channel Islands National Marine Sanctuary, California, USA (hereafter the Channel Islands) provide an opportunity to improve our understanding of population-level MPA effects. A network of protected areas covering approximately 20% of the Islands’ waters was put in place in 2003 (Kirlin et al. 2013). The network has been used as a model case study in protected area design around the world (Botsford et al. (2014) and references therein). We use data from the first 14 years of protection 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. 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 primary methods consist of a spatially-explicit bio-economic simulation model and a Bayesian difference-in-difference regression. We use the simulation model to provide theoretical context for our empirical results. The regression provides our estimate of the population-level conservation effect of the Channel Islands MPAs. All analysis were conducted in R (R Core Team 2019). Our difference-in-difference model was fit using Stan (Carpenter et al. 2017) using 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 supporting information (SI).

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 simulation model consists of 50 patches with wrapped edges. For any one simulation we 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). The population begins at unfished equilibrium. After fishing effort is applied, each simulation is run to equilibrium with and without the selected MPA design (holding all else constant). In each time step, we measure the difference in biomass densities between the scenario with and without the MPAs to calculate the population effect of the MPAs over time. Simulation results provide a library of plausible MPA effects for a range of biological and economic assumptions. One set of simulations is specifically designed to reflect the dynamics of the Channel Islands. We only include species of the same genus as those targeted by fishing in the Channel Islands, restrict fishing pressure to be mostly moderate to low, and cap the MPA size at 20% of the population’s range (a likely upper end to the effective MPA size in question, Rassweiler et al. (2012)).

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. 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). 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 the concepts explored in 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. Targeted species in the Channel Islands include fin-fish such as 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). 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. This identification strategy controls 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 would be 10%.

The simplified form of this model is

\[
d_i \sim \text{Gamma}(e^{\beta_0 + \beta_1 T + \beta_2 MPA_i + \beta_3 T_i MPA_i + B^c X_i + B^s S_i}, \text{shape}, \text{scale})
\]  

(1)

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. \(B^c\) is a vector of coefficients for additional control variables in matrix \(X\) such as water visibility and observer experience. \(B^s\) is a vector of hierarchical coefficients for each sampling location \(S\), 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 (Table.2).

Results

Our Channel Islands-specific simulation provides a set of outcomes that can feasibly bound our expectations for the empirical effects of the MPA network. 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 0.23, and a median age at maturity of 4 years, and a mix of exploitation histories, ranging from low to high (but mostly relatively low) (Alonzo et al. 2004; Dick et al. 2017). While a wide range of MPA effects are plausible, from 0% to upwards of 150%, the median simulated effect size for this stylized version of the Channel Islands after over ten years of protection was 10% (Fig.4).

We compared this range of plausible outcomes to the empirical data. 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) 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.
These response ratios cannot, however, be used as a definitive indicator of population effects of the MPAs. 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. To illustrate this problem, we paired our simulated Channel Islands response ratios to the estimated posterior probability distributions of the empirical Channel Island response ratios by matching the patterns in the empirical response ratios. 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 only moderate, adult movement is low, larval dispersal is high, and displaced fishing effort concentrates around the border of the MPAs.

Our empirical difference-in-difference regression provides a different perspective on population-wide 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.

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 persistently high response ratios suggest that despite overall decreases in targeted biomass densities inside and outside MPAs relative to pre-MPA measurements, the MPAs may still be providing protection within their borders. But, these response ratios are not necessarily an indicator of broader population-level effects. The difference-in-difference strategy presents an alternative identification strategy. It is not without its own strict caveats, but provides 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 positive signal from 2012-2017. After 14 years of MPA protection 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.

How can we explain this result? 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 (e.g. concentration of fishing mortality, Halpern et al. (2004)). The implication of this is that total catches will scale with the size of the available population.

Alternatively, fishers can pursue a “constant-catch” strategy, where 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 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 is an important and often overlooked possibility, 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 (SI Fig.S1) which indicates that a negative MPA effect caused by a constant-catch fishing strategy is unlikely. However, some of the most common targeted species in the Channel Islands, such as blue rockfish and copper rockfish, have seen dramatic increases in reported catches in the Santa Barbara region since the year 2010 (although other such as California sheephead have seen declines relative to pre-MPA catch level). While we include catch histories in our regression, to the extent that these increases in catches are due to external market forces, the disappearance of clear positive population-level MPA effects estimated by our model could be due to exogenous increases in fishing pressure overwhelming any population-level increases caused by the MPA network.

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 2019). The targeted group is made up mostly of fishes with cold-water affinities. We hypothesize that the recent evidence for a decline in densities of targeted species is primarily due to environmental conditions that disproportionately affected the targeted group.
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 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.

Trophic cascades are another possible explanation for our equivocal results. 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 (SI Fig.S42). 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.

Our finding of small MPA effects in recent years is therefore likely a result of both changing fishing dynamics
and environmental disturbance. Given the natural variability of marine ecosystems, 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? Our library of simulation results allows us to explore how MPA effects,
and our ability to measure them, might vary with observation error and natural fish recruitment variation
(including the possibility of recruitment regimes). Using a Bayesian difference-in-difference 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 true simulated MPA effect.

The model struggled severely 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 population-level MPA effect of at least 30%. In the
context of the Channel Islands, 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 (Fig.6-A).

Lester et al. (2009) found massively higher densities and biomass inside MPAs than outside [median biomass increases of over 400%]. But, when MPAs affect nearby control sites used in response ratios through biological spillover or concentration of fishing effort, it is entirely possible to 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 Larsen et al. (2019) suggests, there are many potential alternatives for estimating the population 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, 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.

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 fin-fish at the population level may not be possible. In the absence of clear empirical findings, 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. 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 that account for the population within the MPAs (Field et al. 2006) 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 (e.g. Nickols et al. 2019). 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 (Nickols et al. (2019); Kaplan et al. (2019); Ovando et al. (2016); Fig. 4). Educating communities about the challenges of estimating the effects of MPAs can help ensure 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 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, an important question for which extremely little empirical evidence is available (Smith et al. 2006).

MPAs are an important part of the marine resource management toolbox. As the number and size of global MPA networks increase, we must set appropriate expectations for their outcomes and design effective monitoring programs. 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. 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, 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 like difference-in-difference regression 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.

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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 ($\sigma_r$)             | ∈ $0, 0.05, 0.1, 0.2$                                                       |
| Recruitment autocorrelation ($ac_r$)           | ∈ $0, 0.05, 0.1, 0.2$                                                       |
| DD adult movement                              | ∈ $0.25, 1$                                                                 |
| Density-dependence timing                     | ∈ 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                                    | ∈ OpenAccess, ConstantEffort, ConstantCatch                                  |
| Spatial effort model                           | ∈ Uniform, Biomass, Profits                                                  |
| Years into simulation to start MPA            | uniform(5,0.66)                                                              |
| MPA is Larval Source?                         | ∈ TRUE, FALSE                                                               |
| Randomly place MPA?                           | ∈ TRUE, FALSE                                                               |
| Fleet reaction to MPA                         | ∈ Concentrate, Leave                                                        |
| Patchiness                                    | uniform(0.01,0.75)                                                           |
| MPA habitat factor                            | ∈ 1, 4                                                                      |
Table 2: Posterior means and credible interval for key model coefficients. Conditional on the assumptions of the model, the targeted:year_bins coefficients reflect the effect of the MPAs on mean total biomass of targeted finfish in the Channel Islands. targeted indicates whether the species in question is targeted, tex = technician experience, surge is mean reported surge, kelp is mean reported kelp cover, lag catch is the total reported catch for targeted species in the previous year, temp is the mean temperature at a site, temp_dev is the deviation of a temperature observation from the mean temperature for that island in question. 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

| term                              | Mean   | Lower 89th Percentile | Upper 89th Percentile |
|-----------------------------------|--------|-----------------------|-----------------------|
| (Intercept)                       | -2.81  | -3.08                 | -2.54                 |
| targeted                          | 0.06   | -0.12                 | 0.25                  |
| year_bins(2003,2006]              | -0.82  | -1.07                 | -0.56                 |
| year_bins(2006,2009]              | -0.87  | -1.18                 | -0.53                 |
| year_bins(2009,2012]              | -0.84  | -1.16                 | -0.50                 |
| year_bins(2012,2015]              | -0.97  | -1.28                 | -0.62                 |
| year_bins(2015,2018]              | -0.58  | -0.90                 | -0.22                 |
| var_tex                           | 0.20   | 0.05                  | 0.35                  |
| var_tex_2                         | -0.08  | -0.18                 | 0.03                  |
| var_surge                         | 0.09   | 0.00                  | 0.17                  |
| var_kelp                          | -0.06  | -0.11                 | -0.01                 |
| var_lag_catch                     | 0.06   | -0.04                 | 0.17                  |
| var_temp                          | 0.27   | 0.07                  | 0.46                  |
| regional_temp_dev                | -0.22  | -0.39                 | -0.05                 |
| regional_temp_dev_2              | 0.01   | -0.02                 | 0.04                  |
| targeted:year_bins(2003,2006]     | 0.27   | 0.04                  | 0.52                  |
| targeted:year_bins(2006,2009]     | 0.50   | 0.25                  | 0.74                  |
| term                          | Mean | Lower 89th Percentile | Upper 89th Percentile |
|-------------------------------|------|-----------------------|-----------------------|
| targeted:year_bins(2009,2012] | 0.58 | 0.35                  | 0.84                  |
| targeted:year_bins(2012,2015] | 0.29 | 0.02                  | 0.55                  |
| targeted:year_bins(2015,2018] | -0.08| -0.37                 | 0.20                  |

**Figures**

Figure 1: 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.
Figure 2: Centered and scaled trends in biomass densities of targeted and non-targeted fin-fish 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.
Figure 3: 90\% Posterior probability distributions of response ratios for targeted species (x-axis) over time (y-axis) in dark grey. Simulated population-level (pop.) effect on biomass densities matched to empirical response ratios in light grey. 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\% greater 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.
Figure 4: 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.
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 true simulated MPA effect.
Figure 6: 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.